Universidade de Aveiro Departamento de Biologia
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João Luís Oliveira Carvalho

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Tese apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Biologia, especialização em Recursos Cinegéticos e Aquícolas, realizada sob a orientação científica do Professor Doutor Carlos Manuel Martins Santos Fonseca, Professor Associado com Agregação do Departamento de Biologia da Universidade de Aveiro e coorientação do Doutor Emmanuel Serrano Ferron, Investigador *Ramón y Cajal* do *Departament de Medicina i Cirurgia Animals* da *Facultat de Veterinària* da *Universitat Autònoma de Barcelona*, e da Doutora Nathalie Pettorelli, Investigadora do *Institute of Zoology* da *Zoological Society of London*.

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palavras-chave

Anéis de crescimento, caça troféu, *Capra pyrenaica*, condição corporal, densidade populacional, deterioração do habitat, ecossistemas Mediterrânicos, gestão cinegética, heterogeneidade individual, nutrição, plasticidade fenotípica, sarna sarcóptica

resumo

A caça seletiva (*e.g*. caça troféu) consiste na remoção de indivíduos com determinadas características fenotípicas de uma população selvagem. Apesar de ser uma prática comum, as suas consequências ecológicas e evolutivas são controversas, pois não é claro se as condições ambientais diluem ou intensificam os efeitos desta atividade. Em Espanha, a exploração cinegética do macho-montês (*Capra pyrenaica* Schinz, 1838), através da caça troféu, juntamente com as alterações ambientais registadas na bacia Mediterrânica, podem traduzir-se num efeito indesejado nas características fenotípicas e dinâmica populacional da espécie. Mediante a análise de um extenso repositório de informação individual sobre métricas de crescimento e condição corporal, esta tese tem como principal objetivo determinar os efeitos diretos e indiretos da estratégia de caça, das condições ambientais, da densidade populacional e da sarna sarcótica nas características fenotípicas da cabra-montês. O primeiro estudo (capítulo 2), realizado na Reserva Nacional de Caça de *Els Ports de Tortosa-Beseit*, nordeste de Espanha, confirmou o quão sazonal e diversa é a dieta da cabra-montês em ambientes Mediterrânicos e demonstrou que a heterogeneidade dos ecossistemas Mediterrânicos torna necessária a realização de amostragens sistemáticas para a atualização dos dados relativos à dieta da espécie, um aspeto crucial para o desenvolvimento de diversos caracteres sexuais secundários. Posteriormente, dois estudos observacionais revelaram a importância do *habitat* nos padrões de crescimento dos segmentos córneos do macho montês. O primeiro (capítulo 3) demonstrou que a heterogeneidade individual da longitude dos anéis de crescimento é potenciada por diferenças no *habitat* e que os machos não são capazes de recuperar do crescimento deficitário dos anéis após um eventual período de défices nutricionais. O segundo (capítulo 4) evidenciou que o aumento da área de pinhal, e consequente diminuição da área de pastagens naturais, é um fator decisivo para o decréscimo contínuo da longitude dos anéis de crescimento ao longo das últimas duas décadas. Este último, sugere também que a extração seletiva de animais com reduzidas taxas de crescimento pode contribuir para a mitigação dos efeitos da caça troféu. O último estudo (capítulo 5), realizado no Parque Nacional de *Sierra Nevada*, sul de Espanha, revelou que a regulação da condição corporal exercida por aspetos ambientais e populacionais é quebrada por infeções parasitárias contagiosas, como a sarna sarcóptica. Além da sua importância ecológica, os resultados aqui reportados traduzem-se num conjunto de medidas de ampla aplicabilidade para a gestão das populações de cabra-montês. A presente tese reforça a importância das sinergias entre caçadores, gestores de caça e investigadores tendo em vista a sustentabilidade da atividade cinegética e das populações ibéricas de cabra-montês.

keywords

Body condition, *Capra pyrenaica*, game management, habitat deterioration, horn growth segments, individual heterogeneity, Mediterranean ecosystems, nutrition, phenotypic plasticity, population density, sarcoptic mange, trophy hunting

abstract

Size-selective harvesting (*e.g.* trophy hunting) involves removing specific individuals that exhibit desirable phenotypes. The ecological and evolutionary consequences of selective harvesting are controversial because it remains unclear how environmental conditions dilute or strengthen the effects of this activity. In Spain, the trophy hunting of male Iberian ibexes (*Capra pyrenaica* Schinz, 1838), associated with the ongoing environmental changes of the Mediterranean basin, may have undesirable consequences on the phenotypic traits and population dynamics of this species. By analysing a comprehensive hunting inventory of individual body condition, and correspondent individual metrics, gathered from wild Iberian ibex populations, this thesis is aimed at investigating the direct and indirect pathways by which hunting strategy, environmental conditions, density-dependence factors and diseases (*e.g*. sarcoptic mange) influences the phenotypic traits of Iberian ibex. The first study (chapter 2), carried out in the *Els Ports de Tortosa-Beseit* National Hunting Reserve, northeast Spain, showed that ibexes diet includes a wide range of plant species, that both diet quality and composition follows a seasonal pattern driven by landscape heterogeneity and that the diversity of ibex diet, together with the heterogeneity of Mediterranean ecosystems, hamper the use of remotely sensed products (*e.g*. Normalized Difference Vegetation Index) to predict dietary features, *i.e*. systematic faecal samples are necessary to update the nutritional condition of ibex individuals. Then, two long-term observational studies highlighted the importance of habitat characteristics on the horn growth patterns of male ibexes. The first study (chapter 3) showed that habitat fostered significant horn growth differences among males and confirmed that compensatory horn growth does not occurs in male ibexes. The second study (chapter 4) demonstrated that pine forest encroachment accounted for the decrease of annual segments length over the last two decades and suggested that the selective removal of slow-growing, small-horned males could be important to mitigate the undesirable consequences of trophy hunting. The last study (chapter 5), carried out in the *Sierra Nevada* National Park, south Spain, indicated that the bottom-up regulation of body condition is disrupted by highly infectious parasitic diseases, such as the sarcoptic mange. Apart from representing an important scientific contribution towards a better understanding of Iberian ibex ecology, the results of this thesis have great implications for the management of Mediterranean ungulates and open a direct venue for scientific cooperation and collaborative planning. The synergies between hunters, game managers and researchers are of utmost importance to achieve the long-term sustainability of Iberian ibex populations.

Declaro que esta tese é integralmente da minha autoria, estando devidamente referenciadas as fontes e obras consultadas, bem como identificadas de modo claro as citações dessas obras. Não contém, por isso, qualquer tipo de plágio quer de textos publicados, qualquer que seja o meio dessa publicação, incluindo meios eletrónicos, quer de trabalhos académicos.

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CHAPTER 1 Introduction

* Southern area of the *Els Ports de Tortosa-Beseit* National Hunting Reserve, NE Spain. Photo: João Carvalho.

1.1. General introduction

Ungulates have played a major role in the course of Human evolution and civilization (Diamond, 1997). They occur across all continents (with the exception of Antarctica) and are found naturally in a variety of habitats (Danell *et al.*, 2006). Initially hunted for food and fur, ungulates became of great social and cultural interest over the past 11,500 years (Larson & Fuller, 2014). During the Classical and the Middle Ages, apart from providing valuable products, domesticated ungulates provided long-distance transportation and military assistance, which was pivotal to the spread of Indo-European culture. Nowadays, the emergence of a culture of hornography has proved wild ungulates (hereafter, ungulates) to be important assets for the ecotourism and hunting industry (Leader-Williams *et al*., 2001; Ogutu, 2002; Simon, 2017). From an ecological perspective, ungulates can be considered ecosystem engineers (*sensu* Jones *et al*., 1994) as they modulate the amount and the availability of resources by shaping the structure and function of natural landscapes (Hester *et al*., 2006). They are also important in sustaining large carnivore populations and in contributing to reduce human-carnivore conflicts (Chapron *et al*., 2014). Ungulates are therefore crucial to maintain the integrity of ecosystems as they influence both biotic and abiotic processes (Fritz *et al*., 2011).

In contrast to the largest ungulate species (body mass > 100 kg) found in Africa and south Asia (Ripple *et al*., 2015), ungulates of the Holarctic realm are experiencing an ongoing increase in their numbers and geographical distribution (Apollonio *et al*., 2010). Various factors have been involved in this demographic burgeoning, such as socio-economic changes (*e.g*. rural exodus), loss of predators, re-naturalization of the habitats and reintroduction programs for both conservation and hunting purposes (Acevedo *et al*., 2011; Putman *et al*., 2011; Milner *et al*., 2014; Valente *et al*., 2017; Carvalho *et al*., 2018). The negative impacts of ungulate expansion include, among others, damage to forestry and agriculture, increased involvement in vehicle collisions, dissemination of vector-borne and zoonotic diseases, and deleterious effects on

the vegetation structure and dynamics (Côté *et al*., 2004; Gortázar *et al*., 2006). On the other hand, the upsurge of ungulate populations may have beneficial effects such as the increase of genetic diversity, the restoration of trophic networks and the increment of economic benefits mainly due to ecotourism and/or hunting harvest opportunities (*e.g*. trophy hunting, **Box1**, **Figure 1**). The expansion of ungulates represents therefore a conservation and management challenge (Bueno *et al*., 2010; Cromsigt *et al*., 2013; Perea *et al*., 2014).

Box 1 – Trophy hunting contribution to regional economies and biodiversity conservation

Trophy hunting occurs worldwide and represents one of the most common examples of size-selective harvesting. When focused on wild ungulates, it consists on harvesting males with well-developed horn-like structures, such as horns, antlers or tusks. If poorly regulated, trophy hunting can be harmful for the target populations (Mysterud, 2014); however, if it is under strict management protocols, it can be self-sustainable and might generate important revenues for the conservation of hunted populations and/or endangered species (Leader-Williams, 2009), particularly in areas where ecotourism is not economically or politically viable (Lindsey *et al*., 2006). For instance, Lindsey *et al*., (2007) estimated that trophy hunting in sub-Saharan Africa produced revenues of approximately US$201 million per year. In South Africa alone, the gross revenues from trophy hunting reached US$68 million, in 2012 (Di Minin *et al*., 2016). In Arizona, North America, permits to hunt a bighorn ram (*Ovis canadensis*) ensured an income of US$5.7 million, between 1984 and 2006 (Hedrick, 2011). Twenty-five years ago, red deer (*Cervus elaphus*) hunting in Scotland generated more than £5 million annually (Reynolds & Staines, 1997). These values are likely to be higher today. Paradoxically, limited trophy hunting has contributed to the recovery of endangered ungulate populations.

Box 1 – Trophy hunting contribution to regional economies and biodiversity conservation (Continue)

For example, a conservation program based on limited trophy hunting succeeded in increasing the population of the endangered markhor (*Capra falconeri*) from 200 to 3,500 in Pakistan (U.S. Fish and Wildlife Services, 2014). Although this species is currently assessed as Near Threatened (but as Endangered between 1994 and 2008), the hunting of some mature males is supported by the *Caprinae* Specialist Group of the International Union for Conservation of Nature. Recent studies also support the contention that trophy hunting of ungulates is a viable tool for the conservation of top predators (Kachel *et al*., 2017). Green hunting, *i.e*. the practice of immobilize wild animals with tranquilizer dart guns has emerged as an alternative, however, the economic importance of this modality is still low in comparison to trophy hunting (Loveridge *et al*., 2006).

Here, I provide a spatial explicit overview of trophy prices based on the world scale analysis carried out by Palazy and colleagues (2011). This example is purely illustrative and does not consider trophy fees variations between hunting companies and governments. Please note that the value of trophies also varies in accordance with demand or perceived demand and that local, national and international hunters may use different formulas to calculate trophy prices (Sarasa, 2013). Notwithstanding these sources of variation, our example sets out the potential contribution of trophy ungulates for regional economies and conservation initiatives in remote regions.

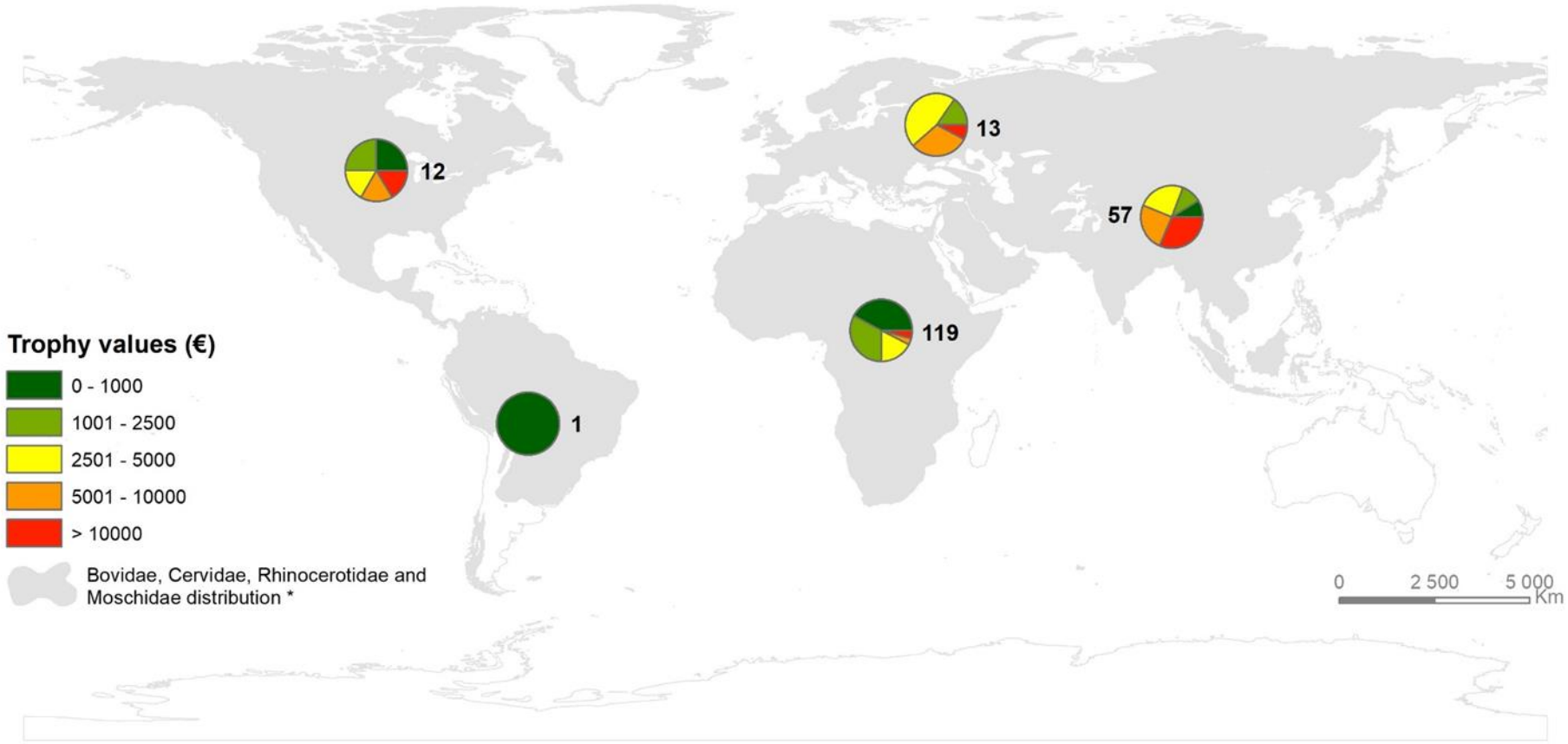

Figure 1. A worldwide overview of trophy prices based on the analysis of Palazy and colleagues (2011). The authors examined the value of 202 ungulate species belonging to one of the following families: *Bovidae*, *Cervidae*, *Rhinocerotidae* and *Moschidae*.

The cultural, ecological and socio-economic relevance of ungulates reinforces the importance of understanding how biotic and abiotic factors rule the dynamics of their populations, as well as the variation of life-history strategies and traits among species, populations and among individuals within a population. This cause-effect relationship is, however, far from completely clear because it varies in space and time, it is contingent on a species or genus and its study requires datasets that span a sufficiently long-time frame (Festa-Bianchet *et al*., 2017). Moreover, scientists, conservationists and wildlife managers have to handle increasingly complex interactions fostered by human activities, such as deforestation, agricultural encroachment and extensive overhunting for subsistence and/or sport, to name just a few. Applied ecological research is therefore utterly needed for the management of ungulate populations be up to its conservation and economic goals (Gordon *et al*., 2004).

Hunting could serve several purposes, such as the control of overabundant species (see Quirós-Fernández *et al*., 2017), however, is not able to reproduce the indirect effects of natural predation on population dynamics (Ordiz *et al*., 2013). Moreover, if directed to specific individual characteristics, this activity can lead to evolutionary and/or phenotypic changes in the life-history traits of ungulates (Festa-Bianchet, 2003; Fenberg & Roy, 2008; Allendorf & Hard, 2009; Darimont *et al*., 2009; Festa-Bianchet, 2016). The demographic and evolutionary effects of size-selective harvesting on wildlife populations have been recognized since the early 20th century (Rutter, 1902). The interest on the effects of size-selective harvesting on ungulates arose one hundred years later, when a significant decline of horn size and body mass of bighorn males (*Ovis canadensis*) was ascribed to hunter selection (Coltman *et al*., 2003). Until then, the consequences of size-selective harvesting on ungulates were mainly focused on the direct effects on population growth (**Figure 2**; Mysterud, 2014).

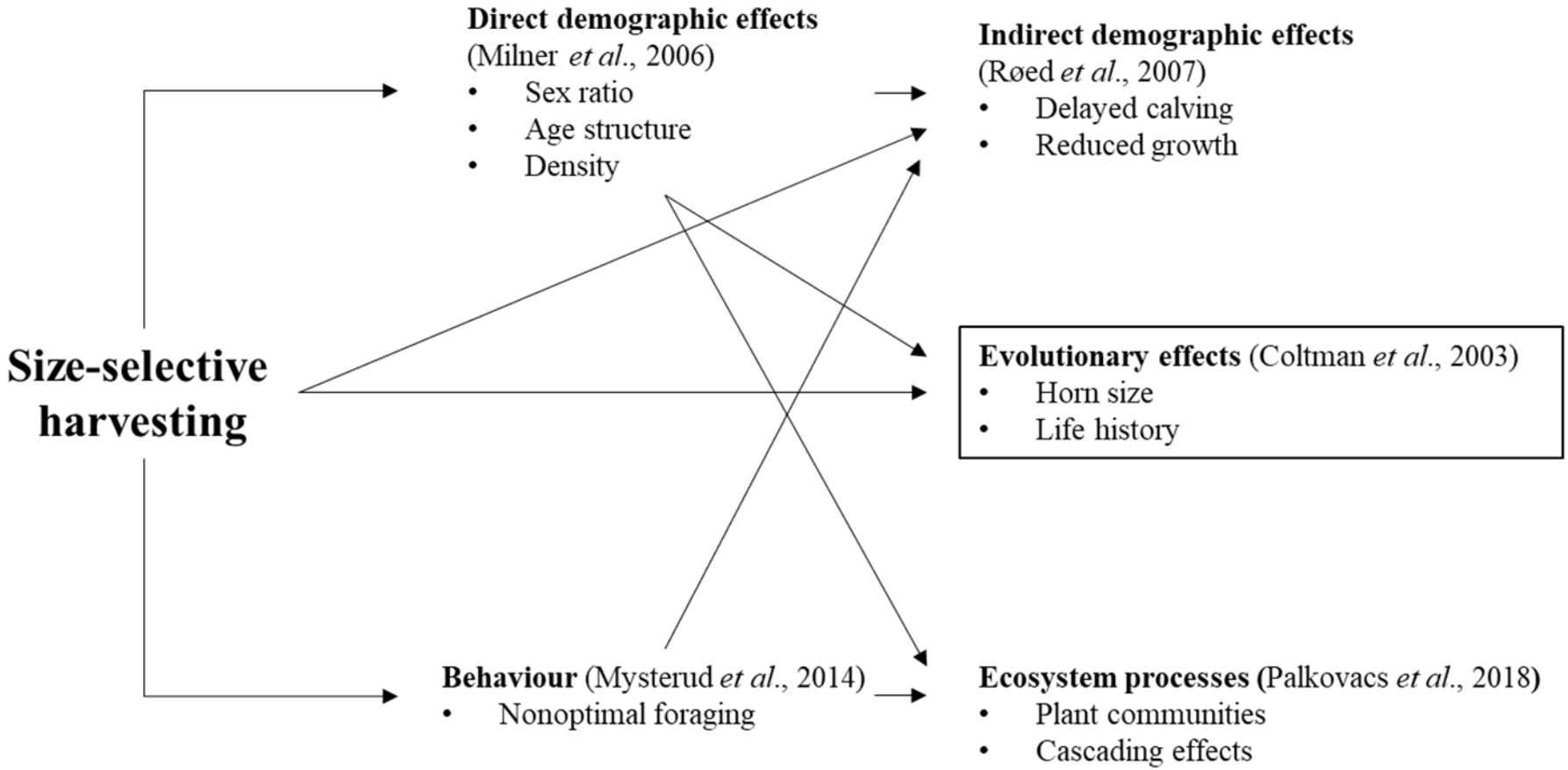

Figure 2. The direct and indirect pathways by which size-selective harvesting affects wild ungulate populations. Adapted from Mysterud (2014).

The evolutionary effects of harvest-based selection on ungulates now attracted the attention of ecologists and evolutionary biologists (**Box 2**). A great body of literature, focused on the genetic basis of phenotypic traits, were however the target of a deal of criticism because did not consider a myriad of individual, population and environmental factors that may counterbalance, weaken or exacerbate the side effects of size-selective harvesting (Heffelfinger, 2018a, b; see also Kardos *et al*., 2018). This missing link will contribute to shed light on the direct and indirect pathways by which size-selective harvesting, environmental conditions and density-dependency affect specific phenotypic traits, such as body and horn size. One of the most consensual determinants of individual fitness is the nutritional condition (*sensu* Harder & Kirkpatrick, 1994). Nutrition determines several aspects of ungulates life-history (Barboza *et al*., 2009), directly affecting ungulates population dynamics (Owen-Smith & Mills, 2006). Nutritional constraints entail, for example, a decrease in the survival of neonates (Monteith *et al*., 2014), an increase in the age of primiparity (Festa-Bianchet *et al*., 1995), a decrease in the pregnancy rate of adult females (Hamel *et al*., 2010) and, ultimately, a decrease in adult survival (Bishop *et al*., 2005). Nutrition also influence the development of phenotypic traits, such as the horn growth of mountain sheep (Pigeon *et al*., 2016; Monteith *et al*., 2018) and the antler growth of elk (*Cervus canadensis*; Wang *et al*., 1999), red deer (Kruuk *et al*., 2002) and caribou (*Rangifer tarandus*; Mahoney *et al*., 2011). Nutrition is therefore an insightful ecological indicator that is closely tied to climate and local weather patterns, habitat characteristics, population abundance and/or health status, as evidenced by several studies carried out in different populations at different latitudes (Pettorelli *et al*., 2005; Cook *et al*., 2013; Santos *et al*., 2018). The implementation of appropriate management strategies to ensure the sustainability of hunted populations is therefore strictly dependent on understand the ecological and anthropogenic processes that affect the nutritional status of ungulate populations (Monteith *et al*., 2018).

Most ungulates are long-lived, so the analysis of long-term datasets may provide enough support to alleviate the ecological and evolutionary impacts of poor management. Long-term field studies are allowing us to understand that phenotypic trait variations, particularly, body and horn growth variations, are

caused by a plethora of interactive factors (see **Table 1** at the end of this chapter). Yet, the lack of a serious long-term commitment of funding agencies discourage many years of intense monitoring and ambitious plans (Clutton-Brock & Sheldon, 2010; Festa-Bianchet *et al*., 2017). Much of what is known about the impact of environment and size-selective harvesting on the dynamics and phenotypic traits of ungulates remain confined to some regions and habitats. The spatial and ecosystem coverage of these studies is largely biased (**Box 2**, **Figure 3**). We still lack studies of how human practices and environmental conditions influence the life-history traits of trophy hunted ungulates inhabiting Mediterranean ecosystems, where climate, phenology and management regimes differ from those recorded in North America and central/ northern Europe. Climate warming has intensified the drying of the Mediterranean basin over the last five decades (Büntgen *et al*., 2017). Recent climatic models show that this phenomenon is expected to continue in the following years and predict an increase in the climate variability (Seager *et al*., 2014). Rising temperatures together with decreasing precipitation and agricultural land abandonment influence the landscape configuration by promoting the encroachment of grasslands by drought resistant woody shrubs (Peñuelas *et al*., 2017). These environmental changes are expected to interact with hunting strategy, however, it is unclear if environmental conditions dilute or strengthen the effects of selective harvesting on specific phenotypic traits.

Box 2 – Literature review about the effects of size-selective harvesting and environmental conditions on the phenotype of wild bovids.

I conducted a literature survey for published papers using the Web of Science platform (http://www.isiknowledge.com). The main goal is to provide an overview of empirical field studies that explore the effects of size-selective harvesting, environmental conditions and population characteristics on the phenotype of wild bovids, particularly on the development of horns. This analysis allows to raise some key points resulting from ecological and evolutionary research on this topic, which could be used to support current management plans, to highlight important knowledge gaps and to redirect future research. Search terms included “artificial selection” OR “trophy hunting” OR “size-selective harvest*” OR “population density” OR “environment” AND “horn size” OR “horn volume” OR “horn shape”. The literature survey did not include any time or spatial restriction but I only considered those papers published in English. The search for articles published until 2018 resulted in 46 papers. The documents were screened and a non-exhaustive list of relevant information were summarized (see **Table 1** at the end of this chapter). I report the studied species, the measurements used in the analysis, the region where the study was conducted, the study period, the number of individuals sampled and the main conclusions gathered. Our synthesis yields key insights about the anthropogenic and environmental forces driving horn growth trends.

The genus *Capra* are primarily found in the “old-world” and comprises 6 to 9 wild species (**Figure 4a**). The taxonomy of *Capra* species and subspecies is still being debated (Pidancier *et al*., 2006). This genus is characterized by five male horn morphotypes that are highly sought by trophy hunters. They included the scimitar-shaped horns of *Capra ibex*, the spiral horned *Capra falconeri* or the wrinkled and curved horns of *Capra pyrenaica*, an Iberian endemism and the focus of this thesis.

Figure 3. Spatial location of 30 field studies that analyzed the effects of size-selective harvesting and/or environmental conditions and/or population characteristics on the horn growth of wild bovids.

The Iberian ibex (*Capra pyrenaica* Schinz, 1838; **Figure 5**) is a medium-sized ungulate endemic to the mountains of the Iberian Peninsula (Pérez *et al*., 2002; Acevedo & Cassinello, 2009). This species is characterized by a remarkable sexual dimorphism (Fandos, 1991). Males are larger and heavier than females and bear well-developed horns that are used to establish dominance hierarchies amongst them (Geist, 1966). The Iberian ibex populations are currently established in most mountain ranges of Spain (**Figure 4b**). In the mid-1990s, some individuals (subspecies *C. p. victoriae*) naturally dispersed from Galicia, NW Spain, and recolonized the *Peneda-Gerês* National Park, Portugal, one century after its local extinction (Moço *et al*., 2006; Fonseca *et al*., 2017).

The International Union for the Conservation of Nature now recognizes four subspecies (*C. p. victoriae*, *C. p. hispanica*, *C. p. pyrenaica* and *C. p. lusitanica*), that are characterized by differences in body size, horn size and shape, and coat color (Cabrera, 1911). The taxonomic status of Iberian ibex is still being discussed because is based on morphological criteria that can vary within populations and are driven by sexual and environmental selection (Clouet, 1979; Acevedo & Cassinello, 2009). Of the four subspecies, only two subsist (*C. p. victoriae* and *C. p. hispanica*). The subspecies *C. p. pyrenaica* became extinct a few years ago, while the subspecies once found in Portugal, *C. p. lusitanica*, went extinct at the end of 19th century (Pérez *et al*., 2002). Several reasons such as illegal hunting, habitat deterioration and fragmentation, increasing presence of domestic livestock and severe sarcoptic mange outbreaks have been pointed out as the main causes for the extinction and decline of Iberian ibex populations over the last centuries (Granados *et al*., 2001). The genetic isolation and the low reproductive rates of Iberian ibex make this species particularly vulnerable to population fluctuations due to environmental variations and human pressure (Shackleton, 1997). Currently, despite prevailing threats (*e.g*. population overabundance, disease outbreaks, competition with livestock and invasive ungulates), the subspecies *C. p. victoriae* (present in the N of Portugal and N-NW of Spain) and *C. p. hispanica* (S of Spain) are experiencing an ongoing increase in number and distribution (Acevedo *et al*., 2007a; Fonseca *et al*., 2017). The species was also recently

reintroduced in the French Pyrenees, after a century of absence. However, the present situation of Iberian ibex populations diverges. Although considered as Critically Endangered in the Portuguese Red Data Book (Cabral *et al*., 2005), the trophy hunting of male ibexes is an important source of income in Spain. This activity is a well-established tradition in this country and the management of Iberian ibex populations is partially focused on the production of large-horned males (Pérez *et al*., 2011a). Iberian ibex horns have particular characteristics that make them highly sought by sport hunters. They present unique curvature features (*i.e*. Iberian ibex horns generally curve out and up and then back) that depend on subspecies and populations. For instance, in *C. p. victoriae*, horn tip curves up, while in *C. p. hispanica*, horn tip curve down (Pidancier *et al*., 2006).

In Spain, the Iberian ibex has been the most coveted trophy among all game species. As the *C. p. victoriae* bear longer and thicker horns than *C. p. hispanica*, this subspecies tends to be sought more often by hunters and, therefore, is more expensive (Sarasa, 2013). Although there are no reliable estimates of revenues produced by the size-selective hunting of male ibexes, auction results revealed that the starting price for *C. p. victoriae* is approximately €5,650 and for *C. p. hispanica* is approximately €3,120 (Sarasa, 2013). Trophy males can reach extraordinarily high values. A recent record was stablished in 2012, when a trophy hunter paid approximately €120,000 for a trophy hunted at sierra de *Alta Coloma*, *Jaén*, Spain. With a final score of 311.47 points, attributed by the *Consejo Internacional de la Caza*, this male is a "record book" trophy. In the same year, another hunter paid €77,500 for a male hunted at *Riaño*, *Castilla y León*, Spain. This value includes the auction hammer price (€34,500) and the final score-based price (€43,000).

During the last decades, the Iberian ibex has caught great scientific interest and the number of studies on different subjects piled up (browsing impacts: Perea *et al*., 2015; endocrine system and horn growth: Toledano-Díaz *et al*., 2007 and Santiago-Moreno *et al*., 2012; habitat selection and space use: Refoyo *et al*., 2016 and Viana *et al*., 2018; interspecific relationships: Acevedo *et al*., 2007b; parasitology: Pérez *et al*., 2006; population dynamics: Fandos *et al*., 2010a). However, comparative studies and applied research aiming to assess the effects of management practices, environmental and population

characteristics on the life-history traits of Iberian ibex populations are still scarce, which can jeopardize the effective management of hunted populations (but see Fandos *et al*., 1995; Pérez *et al*., 2011a).

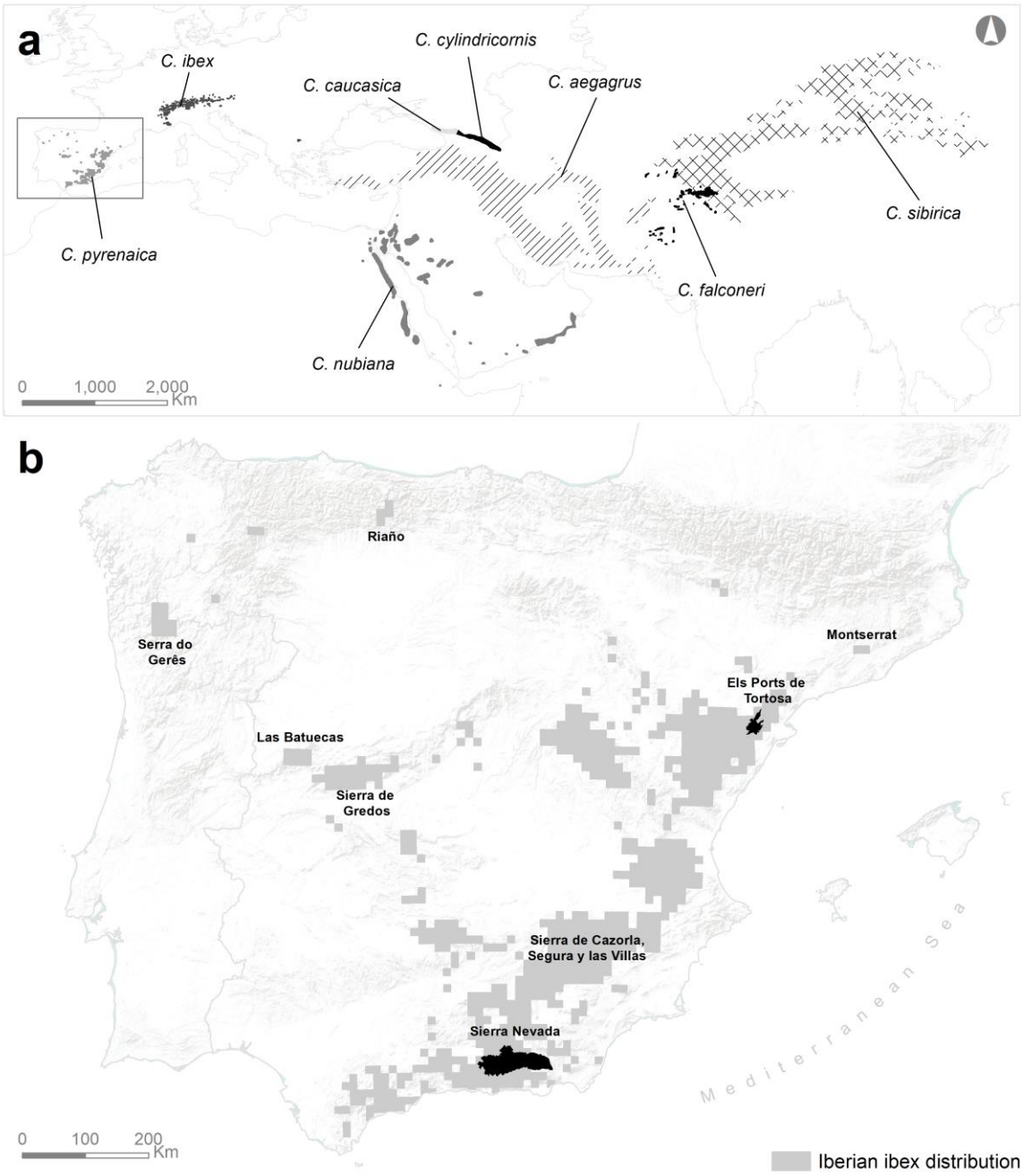

Figure 4. Geographical distribution of wild populations of the genus *Capra* based on the International Union for Conservation of Nature **(a)**, and the detailed geographical distribution of Iberian ibex (*Capra pyrenaica*) populations **(b)** based on the *Atlas de Mamíferos de Portugal* (Fonseca *et al*., 2017) and *Atlas y Libro Rojo de los Mamíferos Terrestres de España* (Granados *et al*., 2007). Presence data refer to grid cells, Universal Transverse Mercator 10x10 km^2.

Figure 5. Male ibex inhabiting a typical Mediterranean area. The annual horn growth segments that characterizes their wrinkled horns are clearly distinguishable. Photo: Xavier Fernández-Aguilar.

1.2. Aims

Wild ungulates are exposed to a myriad of interactive selective pressures. As broad generalizations about the phenotypic side-effects of these pressures can be counterproductive (Heffelfinger, 2018a), studies conducted at population level are increasingly relevant. Here, I take advantage of a rare and vast repository of data on age, sex and morphology of harvested male ibexes in two study areas of mainland Spain, the *Els Ports de Tortosa-Beseit* National Hunting Reserve (**Figure 4b**), NE Spain, and the *Sierra Nevada* National Park (**Figure 4b**), SE Spain, to shed light on how the interaction between management practices, environmental variations and population density drives species' phenotypic traits. Even though harvest data is potentially biased (*e.g*. hunting regulations impose measurement requirements that direct hunters to specific phenotypes, Pelletier *et al*., 2012), an accurate analysis of large sample

sizes collected over decades is pivotal to improving our knowledge about species' ecology (Festa-Bianchet, 2016; Coulson *et al*., 2018).

Specifically, the applied outcomes of this thesis are:

- To assess how landscape heterogeneity relates with the diet quality and composition of Iberian ibex, as nutrition is an important determinant for horn development (Monteith *et al*., 2018), and to validate the use of cost-effective and amenable tools to track and predict dietary features;

- To describe horn growth patterns of male ibexes and explore the direct and indirect pathways by which hunting strategy, environmental conditions, density-dependency and disease affect horn size and body condition of wild ibex populations;

- To provide a scientific basis that support informed decisions regarding the management of hunted Iberian ibex populations.

1.3. Hypothesis

Overall, the research approach relies on testing three general hypotheses, namely (please note that each hypothesis is detailed throughout the thesis chapters):

1. I hypothesize that diet quality and composition of Iberian ibex are related to ecosystem parameters such as vegetation characteristics and habitat structure, *i.e.* dietary parameters can be tracked simply by using satellite-based products;

2. I hypothesize that horn growth patterns and trends are shaped by the interactive effects of hunting strategy, environmental conditions and population density;

3. I hypothesize that the negative effects of disease on body condition, an important aspect for horn development, can be mitigated by favorable environmental conditions.

1.4. Structure of the thesis

These three general hypotheses were tested in each of the following independent, but related chapters. Each chapter represents a manuscript that was published/submitted to an international peer-reviewed journal.

Chapter 2

Carvalho, J., López, H.F., Ibáñez, M., Filellac, J.B., Valldeperes, M., Forcadell, J.M., Olivé-Boix, X., Lavín, S., Pettorelli, N., Fonseca, C. & Serrano, E. (under revision). **Predicting the diet quality and composition of a mountain ungulate from satellite imagery**. Ecological Indicators.

Chapter 3

Carvalho, J., Eizaguirre, O., Pérez, J.M., Mentaberre, G., Lavín, S., Fandos, P., Olmo, J.R., Oliver, X., Torres, R.T., Fonseca, C., Pettorelli, N. & Serrano, E. (2017). **Evidence for phenotypic plasticity but not for compensatory horn growth in male Iberian ibex**. Mammalian Biology, 87, 101-106, doi: 10.1016/j.mambio.2017.06.003.

Chapter 4

Carvalho, J., Büntgen, U., Pettorelli, N., Mentaberre, G., Olivé-Boix, X., Eizaguirre, O., Pérez, J.M., Fandos, P., Torres, R.T., Lavín, S., Fonseca, C. & Serrano, E. (under revision). **Habitat management is key to the sustainability of trophy hunting in Mediterranean ecosystems**. Ecological Applications.

Chapter 5

Carvalho, J., Granados, J.E., López-Olvera, J.R., Cano-Manuel, J., Pérez, J.M., Fandos, P., Soriguer, R.C., Velarde, R., Fonseca C., Ráez, A., Espinosa, J., Pettorelli, N. & Serrano, E. (2015). **Sarcoptic mange breaks up bottom-up**

regulation of body condition in a large herbivore population. Parasites & Vectors, 8:572, doi: 10.1186/s13071-015-1188-4.

Chapter 2 describes the diet quality and composition of male ibexes inhabiting a Mediterranean ecosystem and is aimed to validate the association between satellite-derived products and the dietary features of the species. Predicting the diet quality and composition from satellite remote sensing techniques provides a cost-effective method to track the space-time availability of food resources. This is an important step towards an effective management of Iberian ibex populations as this species roam inaccessible habitats, where fieldwork poses many logistical challenges.

Chapters 3 and **4** are complementary. Chapter 3 deepens our knowledge about horn growth patterns of male ibexes and tests if they are able to compensate from the growth depression resulting from periods of food restriction. Chapter 4 adds four years of data to those available in chapter 3 and has a very applied focus. Chapter 4 investigates how hunting strategy, environmental conditions and population density drive horn growth patterns of males' ibexes, and set specific management measures related with habitat structure and hunting strategy.

Chapter 5 shows that the expected association between forage availability and body condition (*i.e.* bottom-up regulation) could be disrupted by highly contagious infestations such as the sarcoptic mange. This chapter is related to the previous chapters because body condition is related with the growth and maintenance of well-developed secondary sexual characters.

Finally, in the **Chapter 6**, the key findings are summarized and the future prospects are discussed.

Table 1. Effects of size-selective harvesting, hunting regulations, population characteristics and environmental conditions on the horn growth of wild bovids. The works are referred by the year of publication. (*) denoted that the information provided is not completely clear.

Species	Horn measurements	Study area	Period	Data	Main findings	Reference
Dall's sheep (*Ovis dalli*)	Annual horn growth, diameter of each annual segment, horn volume	Alaska's mountain ranges, Alaska, USA	3 years (1968 - 1970)	570 males	The percent of glacial cover was positively associated with horn size, whereas high sheep densities had a negative effect on the size of this trait.	Heimer & Smith (1975)
Dall's sheep (*Ovis dalli*)	Annual horn growth	Saint Elias Mountains, Yukon, Canada	2 years (1966 - 1967) *	567 horn annuli from 53 males and 49 females	Horn growth was affected positively by the spring precipitation. Younger individuals were more prone to be affected by unfavorable conditions than older males.	Bunnell (1978)
Bighorn sheep (*Ovis canadensis*)	Horn length	Ram Mountain, Alberta, Canada	20 years (1972 - 1991)	NA	The reduction of ewe density increases trophy ram size.	Jorgenson *et al*., (1993)
Iberian ibex (*Capra pyrenaica*)	Horn length, annual horn growth	*Sierras de Cazorla*, *Segura y Las Villas* Natural Park, *Jaén*, Spain	4 years (1980 - 1983)	368 horn annuli from 47 males	Environmental conditions were related to horn growth variation; however, horn tip length is not influenced by variations in resource availability.	Fandos (1995)
Cantabrian chamois (*Rupicapra pyrenaica parva*)	Annual horn growth	Cantabrian Mountains, Cantabria and Asturias, Spain	9 years (NA)	198 males and 142 females	Horn growth was positively correlated with annual precipitation.	Pérez-Barbería *et al*., (1996)
Bighorn sheep (*Ovis*	Horn length	Ram Mountain, Alberta, Canada	27 years (1971 - 1997)	179 males ≥ 3 years old	Spring precipitation had no apparent effect on horn growth. Higher bighorn	Jorgenson *et al*., (1998)

***canadensis*)**					densities affect negatively horn development.	
Mountain goat (*Oreamnos americanus*)	Horn length, horn base circumference	Caw Ridge, Rocky Mountains, Alberta, Canada	10 years (1988 - 1997)	51 males and 84 females	Precipitation had no apparent effect on horn growth.	Côté *et al*., (1998)
Alpine ibex (*Capra ibex ibex*)	Horn length, length of the first-annual segment	*Belledonne-Sept-Laux Reserve*, *Isère*, France	12 years (1986 - 1998) *	100 males at ages 1-12 years and 84 females at ages 1-14 years	Environmental conditions of the birth year affected the length of the first-annual increment of male horns.	Toigo *et al*., (1999)
Dall's sheep (*Ovis dalli dalli*)	Annual horn growth, basal circumference of each annual segment, horn volume	Southwest Yukon, Yukon. Canada	26 years (1974 - 1999)	2481 males	Summer temperature and precipitation played a major role on the growth of annual horn segments.	Hik & Carey (2000)
Alpine ibex (*Capra ibex ibex*)	Annual horn growth	Grisons, eastern Alps, Switzerland	10 years (1981 - 1990)	3,067 horn annuli from 725 males at ages 1-6 years	Temperature and plant phenology in spring influenced horn growth. No correlation between horn growth and population size was detected.	Giacometti *et al*., (2002)
Bighorn sheep (*Ovis canadensis*)	Horn length, body mass	Ram Mountain, Alberta, Canada	32 years (1971 - 2002)	447 body weight and 395 horn length measurements from 192 males at ages 2-4 years	Unrestricted trophy hunting caused a decline in the mean breeding values of horn length and body mass.	Coltman *et al*., (2003)
Bighorn sheep (*Ovis canadensis*)	Annual horn growth, basal circumference of	Ram Mountain, Alberta, Canada	26 years (1975 - 2000)	182 males at ages 2-9 years	The effect of resource availability on yearly horn growth was dependent on age and individual body mass.	Festa-Bianchet *et al*., (2004)

	each annual segment, body mass					
Alpine ibex (*Capra ibex*)	Annual horn growth	*Gran Paradiso* National Park, *Aosta-Piedmont*, Italy	9 years (1988 - 1997)	378 males at ages 5-15 years	Spring rainfall and high winter temperatures had a positive effect on annuli growth.	von Hardenberg *et al*. 2004
Mountain goat (*Oreamnos americanus*)	Horn length, horn base circumference, body mass	Caw Ridge, Rocky Mountains, Alberta, Canada	13 years (1990 - 2002)	288 goats at ages 1-2 years	Spring forage quality and maternal age affected positively the horn length and the body mass of yearlings. No effects were detected for maternal reproductive status or social rank.	Gendreau *et al*., (2005)
Mouflon (Ovis gmelini musimon)	Horn length, horn base circumference, horn breadth, body mass	*Caroux-Espinouse massif*, *Massif Central*, France	28 years (1976 - 2003)	159 - 329 males (contingent on horn measures)	Habitat loss played a role in the decrease of phenotypic quality. Horn length is less prone to be affected by habitat characteristics than body mass.	Garel *et al*., (2007)
Dall's sheep (*Ovis dalli*)	Annual horn growth, basal circumference of each annual segment	Southern lakes, Pelly Mountains, Ruby Range, and Ogilvie-Mackenzie, Yukon, Canada	42 years (1973 - 2005)	55,565 horn annuli from 8,417 males for length analysis and 50,546 horn annuli from 8,409 males for volume analysis.	Spring weather conditions explained a large proportion of variability in horn growth.	Loehr *et al*., (2010)
Bighorn sheep (*Ovis canadensis mexicana*)	Horn length	Aravaipa Canyon, Arizona, USA	31 years (1980 - 2010) *	NA	The decrease in horn size resulted from a combination of environmental deterioration, inbreeding depression and selective harvesting.	Hedrick (2011)

Bighorn sheep (*Ovis canadensis californiana* and *Ovis canadensis canadensis*)	Horn length, early horn growth	Southern interior and Rocky Mountains, British Columbia, Canada	29 years (1975 - 2003)	3,402 males	Permit type and hunter origin had little impact on horn size of males. Appropriate management strategies may reduce the negative effects of selective hunting.	Hengeveld & Festa-Bianchet (2011)
Iberian ibex (*Capra pyrenaica*)	Horn length	*Sierras de Cazorla*, *Segura y Las Villas Natural Park*, *Jaén*, Spain	22 years (1968 - 1986 and 2001 - 2003)	1,005 males at ages 8-13 years	Age and environmental conditions explained one-fifth of variance in horn length. Higher population densities contributed to the reduction of horn size.	Pérez *et al*., (2011a)
Aoudad (*Ammotragus lervia*)	Horn length	*Sierra Espuna* Regional Park, *Murcia*, Spain	20 years (1980 - 1999)	230 males at ages 4-11 years	Age and environmental conditions explained 53% of variance in horn length.	Pérez *et al*., (2011a)
Alpine chamois (*Rupicapra rupicapra*)	Horn length	Central-Eastern Alps, *Trento*, Italy	5 years (2005 - 2009)	1,685 yearlings	Larger horns were found in calcareous substrates. Snow cover had a negative influence in the horn length of yearling Alpine chamois.	Chirichella *et al*., (2013)
Impala (*Aepyceros melampus*)	Horn length	*Matetsi* Safari Area, Zimbabwe	35 years (1974 - 2008)	1,435 males	Forage availability and population density had no influence on horn length variations. Horn length decreased with distance from national parks.	Crosmary *et al*., (2013)
Greater kudu (*Tragelaphus strepsiceros*)	Horn length	*Matetsi* Safari Area, Zimbabwe	35 years (1974 - 2008)	1,560 males	Forage availability and population density had no influence on horn length variations. The distance to national parks had no effect on horn length.	Crosmary *et al*., (2013)
Sable antelope (*Hippotragus niger*)	Horn length	*Matetsi* Safari Area, Zimbabwe	35 years (1974 - 2008)	1,163 males	Forage availability and population density had no influence on horn length variations. The distance to national parks had no effect on horn length.	Crosmary *et al*., (2013)

					Trophy hunting supported the reduction of horn length.	
Bison (*Bison bison*)	Horn length, horn base circumference	North America	109 years (1900 - 2008)	384 trophy males	No significant long-term trend was recorded for horn size because this species experienced a conservative harvest regime.	Monteith *et al*., (2013)
Muskox (*Ovibos moschatus*)	Horn length, horn base circumference	North America	110 years (1900 - 2008)	399 trophy males	Horn size increased since 1970s due to nutritional and demographic benefits resulting from range expansion through intact habitats.	Monteith *et al*., (2013)
Mountain goat (*Oreamnos americanus*)	Horn length, horn base circumference	North America	111 years (1900 - 2008)	741 trophy males	No significant long-term trend was recorded for horn size because this measure is difficult to judge in the field. Size-selective harvesting is less likely to occur.	Monteith *et al*., (2013)
Bighorn sheep (*Ovis canadensis canadensis*)	Horn length, horn base circumference	North America	112 years (1900 - 2008)	1,191 trophy males	No significant long-term trend was recorded for horn size because this species experienced a conservative harvest regime.	Monteith *et al*., (2013)
Desert sheep (*Ovis canadensis nelsoni*)	Horn length, horn base circumference	North America	113 years (1900 - 2008)	768 trophy males	No significant long-term trend was recorded for horn size because this species experienced a conservative harvest regime.	Monteith *et al*., (2013)
Dall's sheep (*Ovis dalli dalli*)	Horn length, horn base circumference	North America	114 years (1900 - 2008)	323 trophy males	A steepest decline was reported for horn size probably due to size-selective harvesting.	Monteith *et al*., (2013)
Stone's sheep (*Ovis dalli stonei*)	Horn length, horn base	North America	115 years (1900 - 2008)	382 trophy males	A steepest decline was reported for horn size probably due to size-selective	Monteith *et al*., (2013)

	circumference				harvesting.	
Alpine ibex (*Capra ibex ibex*)	Annual horn growth	Eastern Swiss Alps, Switzerland	48 years (1964 - 2011)	42,239 horn annuli from 8,043 males	Spring warmer temperatures fostered annual horn growth.	Büntgen *et al*., (2014)
Bighorn sheep (*Ovis canadensis*)	Horn length, horn base circumference	Sheep River and Ram Mountain, Alberta, Canada	38 years (1974 - 2011)	7,100 males	Favorable environmental conditions caused a rapid horn growth. Selective hunting caused a reduction in horn length and a decrease in the number of trophy rams.	Festa-Bianchet *et al*., (2014)
Bighorn sheep (*Ovis canadensis*)	Horn length, horn base circumference	Alberta, Canada	38 years (1974 - 2011)	7,087 trophy males	Males shot near harvest refuges had longer horns than those males living far from refuges, however, the decline of horn length was pervasive.	Pelletier *et al*., (2014)
Stone's sheep (*Ovis dalli stonei*)	Horn length, annual horn growth, horn base circumference, horn shape	Skeena Region, NW British Columbia, Canada and Peace Region, NE British Columbia, Canada	38 years (1975 - 2012)	12,749 males (3,610 from Skeena and 9,139 from Peace)	Unrestricted hunting had undesirable long-term consequences such as the reduction of trophies.	Douhard *et al*., (2016)
Bighorn sheep (*Ovis canadensis*)	Horn length, horn base circumference	Ram Mountain, Alberta, Canada	40 years (1972 - 2011)	2,295 measures from 497 males and 510 females at ages 2-4 for horn length at ages 2-10 for horn circumference	Selective hunting caused a reduction in horn length. Male recovery is low even when selective hunting ceased.	Pigeon *et al*., (2016)
Bighorn sheep (*Ovis canadensis*)	Annual horn growth	Ram Mountain, Alberta, Canada	42 years (1972 - 2013)	832 horn annuli from 292 males	Horn growth was negatively influenced by high population densities and positively by warm spring temperatures.	Douhard *et al*., (2017)

Bighorn sheep (*Ovis canadensis sierrae*)	Horn size (indexed as the sum of horn lengths and basal circumferences)	Sierra Nevada, California, USA	15 years (2002 - 2016)	175 males	Maternal condition had life-long effects on growth of males. Higher female densities triggered density-dependent effects through nutritional limitations.	Monteith *et al*., (2018)
Alpine ibex (*Capra ibex ibex*)	Horn length, annual horn growth	Eastern Swiss Alps, Switzerland	36 years (1978 - 2013)	44,088 horn annuli from 8,355 males	Hunting regulations mitigated the potentially undesirable evolutionary effects of selective harvesting.	Büntgen *et al*., (2018)

CHAPTER 2 Predicting the diet quality and composition of a mountain ungulate from satellite imagery

* Two ibexes foraging during the summer period in areas above 2000 m a.s.l.. Photo: João Carvalho.

Abstract

Remotely sensed vegetation indices have been widely used in ecological studies as proxies of forage quality. However, the premise that satellite composites directly reflect the dietary features of wild ungulate populations was tested for a very limited number of species and ecosystems.

Using nutritional data from a Mediterranean Iberian ibex (*Capra pyrenaica*) population, we studied the diet quality and composition of male ibexes over a 1-year period and we examined the relationship between two satellite derived products (Normalized Difference Vegetation Index (NDVI) and habitat structure) and three nutritional indicators (fecal nitrogen content, dietary fibers fraction and diet composition), here representing the availability of high-quality forage.

Our results showed that seasonality modulates the feeding behavior of male ibexes and the relationship between diet quality and composition. Fecal nitrogen picked during the spring, while fibers fraction picked during the winter, precisely when the consumption of non-leguminous woody species reached its highest value. Our findings demonstrated that the higher representativeness of accessible forage and an increase in NDVI did not always coincide with increased fecal nitrogen. This relationship is positive, but non-significant, only during the spring, which suggests that the usefulness of satellite-based indices as predictors of diet quality of Mediterranean ungulates depend on the season.

We advocate that the use of satellite products as proxies of diet quality and composition of Mediterranean ungulates must be done with caution. Large-scale data may not adequately represent the scale ungulates actually feed and, therefore, can make habitat management decisions imprecise. The use of imaging spectroscopy with fine spatial and spectral resolution could be an important tool to shed light on the relationship between vegetation metrics and the dietary features of wild ungulates inhabiting highly heterogeneous habitats.

Keywords *Capra pyrenaica*, fecal nitrogen, forage quality, habitat structure, microhistological analysis, Normalized Difference Vegetation Index, nutritional indicators, Spain

2.1. Introduction

Satellite remote sensing products are widely accessible and provide a consistent spatial and temporal coverage of environmental information at biologically meaningful resolution (Pettorelli *et al*., 2014). The Normalized Difference Vegetation Index (NDVI, Pettorelli, 2013) and the Enhanced Vegetation Index (EVI, Huete *et al*., 2002), in particular, have been used in ecological studies as proxies of vegetation quantity and quality (Loe *et al*., 2005; Simard et al., 2014). Though they correlate with aboveground net primary production (Paruelo *et al*., 1997) and plant phenology (Justice *et al*., 1985), the premise that vegetation indices derived from satellite composites directly reflect forage and diet quality of wild ungulates was validated for a very limited number of ecosystems (alpine: Hamel *et al*., 2009; desert: Creech *et al*., 2016; savanna: Ryan *et al*., 2012; temperate forest: Borowik *et al*., 2013). For example, NDVI predicted the availability of high-quality vegetation for alpine herbivores (Hamel *et al*., 2009), has proved its worth as an index of nitrogen content for African herbivores (Ryan *et al*., 2012), and EVI reflected the diet quality of a mountain ungulate inhabiting a highly seasonal environment (Villamuelas *et al*., 2016). The validation of the relationship between satellite-based products and nutritional indicators of forage quality is now recognized as an important step to answer more specific questions related with the feeding behavior, space-use patterns and population dynamics of wild ungulates (Christianson & Creel, 2009). This assumption must be tested in different environmental scenarios to support the biological significance of satellite-based indices and broaden its applicability (Hamel *et al*., 2009)

The Mediterranean basin houses several ungulate species of ecological and socioeconomic relevance and are characterized by unique climate conditions that support complex plant community structures (Rundel *et al*., 2016). To date, no studies assessed the relationship between landscape-level vegetation productivity, habitat structure and the dietary features of wild ungulates living under the environmental regime of Mediterranean arc (but see Santos *et al*., 2018). The validation of this interaction is increasingly relevant for studies on the dynamics of Mediterranean ungulate populations, as the aridity of this ecosystem is increasing (Kelley *et al*., 2012), the growing seasons are

shifting (Burrows *et al*., 2011) and the landscape configuration is changing (Peñuelas *et al*., 2017).

The Iberian ibex (*Capra pyrenaica*) is an iconic and keystone species in the Mediterranean region of the Iberian Peninsula for their role in vegetation dynamics and landscape structure (Perea *et al*., 2015), and their cultural and economic value (Fandos *et al*., 2010b). Currently, Iberian ibex occurs in most mountain ranges of Spain (Acevedo & Cassinello, 2009), where may perform altitudinal movements to track resources availability whenever environmental conditions deteriorate (Viana *et al*., 2018). As the availability and the quality of food resources drive the body condition of wild ibexes (Serrano *et al*., 2011), influence the development of males' horns (Carvalho *et al*., 2017) and determine the movement patterns of the species (Viana *et al*., 2018), the implementation of adequate management plans rely on the space-time quantification of their food resources. Considering that ibexes are characterized by a high feeding plasticity and that the feeding habits of this species are closely related to habitat composition and food availability (Martínez, 1994; Martínez, 2000), we advocate that Iberian ibex is an excellent species to assess if satellite-based information could predict the dietary characteristics of a mixed feeder inhabiting a highly heterogeneous ecosystem. The development of dietary proxies is especially important for ungulates that roam remote and inaccessible habitats, where fieldwork poses many logistical challenges and imply significant risks.

The overarching goal of this study is, therefore, to explore cost-effective procedures able to assess and predict the dietary features of Mediterranean ungulates. Our study is novel as it relates satellite-based products with a complete dietary assessment in terms of diet quality (*i.e*. fecal nitrogen and detergent fibers content) and diet composition (*i.e.* diversity and representativeness of plant species). With few exceptions (see Villamuelas *et al*., 2016), previous studies linked NDVI to one single nutritional indicator, the fecal nitrogen. This could lead to misinterpretations because fecal nitrogen is a proxy of diet digestibility and may not be directly related with diet nitrogen (Gálvez-Cerón *et al*., 2015). Here, we followed a two-fold framework. First, we update the diet quality and composition of a typical Mediterranean population using approximately two hundred fecal samples collected all year round.

Second, we seek to provide biological significance to satellite-based products by analyzing how NDVI and habitat structure might be used to explain the diet quality and composition of Iberian ibexes. The working hypothesis and predictions of our study are summarized as follows. Diet quality and composition follows a seasonal pattern (Hypothesis 1). Based on previous studies, we predict that ibexes respond to the seasonal availability of food resources (Martínez *et al*., 1985; Martínez, 1989; Martínez, 1994). We expect that the representativeness of non-leguminous woody species will be greater in the winter, while the consumption of leguminous woody, forbs and graminoids will decrease from the spring to winter due to natural senescence. As forage digestibility is reduced by higher fiber content, *e.g*. ligneous plants (Van Soest, 1994), we expect that diet quality peaks in the spring and decrease from then on. Although it was never tested for Iberian ibex populations, we hypothesize that seasonality shapes the relationship between diet quality and composition (Hypothesis 2). For instance, plant secondary metabolites, such as tannins, are known to increase nitrogen retention and absorption (Lamy *et al*., 2011). As metabolites content vary seasonally and among plant species, we expect they may influence the relationship between these two nutritional indicators. Finally, we consider that the diet quality and composition of ibexes could be predicted by NDVI and habitat structure (Hypothesis 3). However, we have no clear prediction about the strength and the direction of this relationship, as the heterogeneity of Mediterranean ecosystems may lead to inaccurate estimates of plant productivity and vegetation indices relate primarily to canopy level, which is generally inaccessible to medium-sized ungulates (Huete *et al*., 1985; Huete & Tucker, 1991).

2.2. Material and methods

2.2.1. Study area

This study was carried out in the *Els Ports de Tortosa i Beseit* National Game Reserve (PTB, hereafter). PTB has 28,587 hectares and extends over a rugged and heterogeneous Mediterranean territory located in the eastern edge

of the Iberian system (**Figure 6a**). According to the Köppen–Geiger classification system, PTB is located in the transition between a semi-arid and mesothermal climate (Kottek *et al*., 2006). The eastern face and the base area of the study area are characterized by shrubs of kermes oak (*Quercus coccifera*) and mastic trees (*Pistacea lentiscus*). Degraded evergreen oak grove (*Quercus ilex*) are found through the higher zones, together with Scots pine (*Pinus sylvestris*). The sub-Mediterranean stage are dominated by denser pinewoods of European black (*Pinus nigra*) and Allepo pine (*Pinus halepensis*). Over the last decades, a pervasive conversion of natural pastures and open scrublands into dense woods of pines have been observed (Vargas & Vila, 2005).

2.2.2. Iberian ibex sampling

Fecal samples were collected in the field directly from the rectum of 192 male ibexes, which were legally shot by registered hunters or game rangers between December 2014 and May 2016. The geographical coordinates of each hunted ibex were recorded (**Figure 6b**). The fecal pellets were placed in individual plastic zip bags and transported in a cooler box to the laboratory, where they were mechanically macerated and divided in two portions. One portion was stored in a freezer at - 20°C until the determination of dietary quality, whereas the other portion was kept at room temperature for subsequent microhistological analysis.

2.2.3. Nutritional indicators

Fecal nitrogen (FN) was used as a proxy of dietary quality (Leslie *et al*., 2008), whereas neutral detergent fibers (NDF = cellulose + hemicellulose + lignin), acid detergent fibers (ADF = cellulose + lignin) and acid detergent lignin (ADL = lignin) were used as proxies of diet digestibility (Barboza *et al*., 2009). Here, FN was expressed as a proportion of NDF (hereafter, FNNDF; Ramanzin *et al*., 2017). FN, NDF, ADF and ADL contents were assessed by using near-infrared reflectance spectroscopy (NIRS). The 192 milled samples were thawed

and packed into 35 mm diameter circular cups, with quartz glass window, and scanned from 1100 to 2500 nm using a NIRSystems 5000 scanning monochromator (FOSS, Hillerod, Denmark). Reflectance was recorded at 2 nm intervals as log (1/R), where R represents reflected energy. Each sample was scanned twice, by manually rotating the same cup relative to the previous scan. The data processing and statistical analyses were performed using the *WinISI III* (v.1.6) software. The modified partial least squares (MPLS) method was used to obtain the NIRS calibration equations. External validation was assessed by means of a linear regression between NIRS results and reference data on red deer (*Cervus elaphus*) diets, a species that share diet similarities with the Iberian ibex.

The diet composition of male ibexes was determined by microhistological analysis using a subset of 97 fecal samples evenly distributed throughout the study area (**Figure 6b**). Fecal samples were prepared following the methodological procedure described in Bartolomé *et al*. (1995), with minor modifications. Approximately ten grams of the milled sample were placed in test tubes with 5 ml of HNO3 65%. Then, the test tubes were boiled in a water bath at 80ºC, over 2 minutes. After digestion, the samples were diluted in 200 ml of water and then passed through 1.00-mm and 0.125-mm filters. The 0.125–1.00-mm fraction was spread on glass microscope slides using a 50% aqueous glycerin solution. Cover-slips were then fixed to the slides with DPX microhistological varnish. Three slides were prepared from each sample and were examined under a microscope at 100-400x magnifications, realizing lengthwise traverses. Plant fragments (*e.g.* epidermis, trichomes) were recorded and counted. Until 200 fragments of leaf epidermis were identified in each sample. An epidermis collection of plants sampled in the study area was used to identify plant species or, at least, plant genus. Results have been expressed as the proportion of given plant species or genus over the total of fragments found.

2.2.4 Environmental data

We used the NDVI as an indicator of primary productivity (Petorelli, 2013). The NDVI values were computed from satellite products provided by MODIS (Moderate Resolution Imaging Spectroradiometer, Solano *et al*., 2010, http://modis.gsfc.nasa.gov) at a spatial and temporal resolution of 500 m and 16 days, respectively. The MOD13A1 surface reflectance products corresponding to tile h18.v4 were downloaded from the Land Processes Distributed Active Archive Center (LP DAAC) (ftp://e4ftl01.cr.usgs.gov). A total of 36 scenes from November 2014 and May 2016 were acquired. As FN values relate with short-term dietary quality, we assigned each sample to the value of the nearest 16-day composite period prior the date on which the male ibex was hunted.

The assessment of factors that drive diet quality and composition of ruminants also demand information about the land cover. We therefore downloaded a satellite remote sensing product to perform an up-to-date land cover classification of the study area. A Sentinel-2 Multispectral Instrument Level-2A image (relative orbit number R051, tile number T31TBF) acquired on 6th of May 2017 10:50 am UTC (https://scihub.copernicus.eu/) was visualized and processed using the Sentinel Application Platform (SNAP, http://step.esa.int/main/toolboxes/snap/). The Level-2A images include an atmospheric correction applied to Top-Of-Atmosphere, which is important to enhance the interpretation of satellite images. Ten bands, of a total of 13, with 10 and 20 meters of spatial resolution and a spectral resolution ranging 490 to 2,190 nm were used for classification purposes. We resampled to 10 meters the spatial resolution of the red-edge and SWIR bands to make them compatible with the visible and NIR bands. Our classification region encompasses the area of PTB plus a 1.200 meters buffer where ibexes are likely to roam. We selected a classification scheme that includes 13 classes (**Table 2**). The classes were established using the previous knowledge of the study area and its importance in terms of forage availability and quality. During the classification process, we generated a number of areas of interest (AOI's) to perform the supervised classification of land cover (**Table 2**). The Euclidean distance was used to analyze the spectral signatures of each class and to determine the AOI's subset that presents the highest separability among land use classes. We then

collected a total of 224 points during a field campaign to assess the classification accuracy of the land use map (**Figure 6c**). The number of control points collected per class was weighted according to the spatial representativeness of each land use class (**Table 2**). Land cover was visually identified in the field and assigned to each control point for validation purposes. The geographic coordinates were recorded using a GPS device. Auxiliary information such as Google Earth's high-resolution images, thematic maps from the Spanish National Forest Inventory and elevation were used to assist the visual interpretation of the classification output. The vegetation productivity and habitat structure that characterizes the sample location were inferred for a buffer of approximately 550 hectares. This area was defined based on the minimum home range for the species (Escos & Alados, 1992; Viana *et al*., 2018).

Table 2. Baseline information used during the land cover classification process.

Land use class	Number of areas of interest (AOI's)	Number of pixels (10 meters)	Number of control points
Forests of *Pinus sylvestris*	12	1486	23
Forests of *Pinus halepensis*	7	723	28
Forests of *Pinus nigra*	9	267	
Forests of *Quercus ilex*	7	423	28
Forests of *Fagus sylvatica*	4	59	9
Riverside forests	5	181	9
Shrubland	19	317	32
Grassland	8	182	9
Irrigated crops	5	295	12
Non-irrigated crops	6	741	22
Non-irrigated crops with herbaceous layer	8	771	13
Bare soil	6	308	17
Water	2	363	3

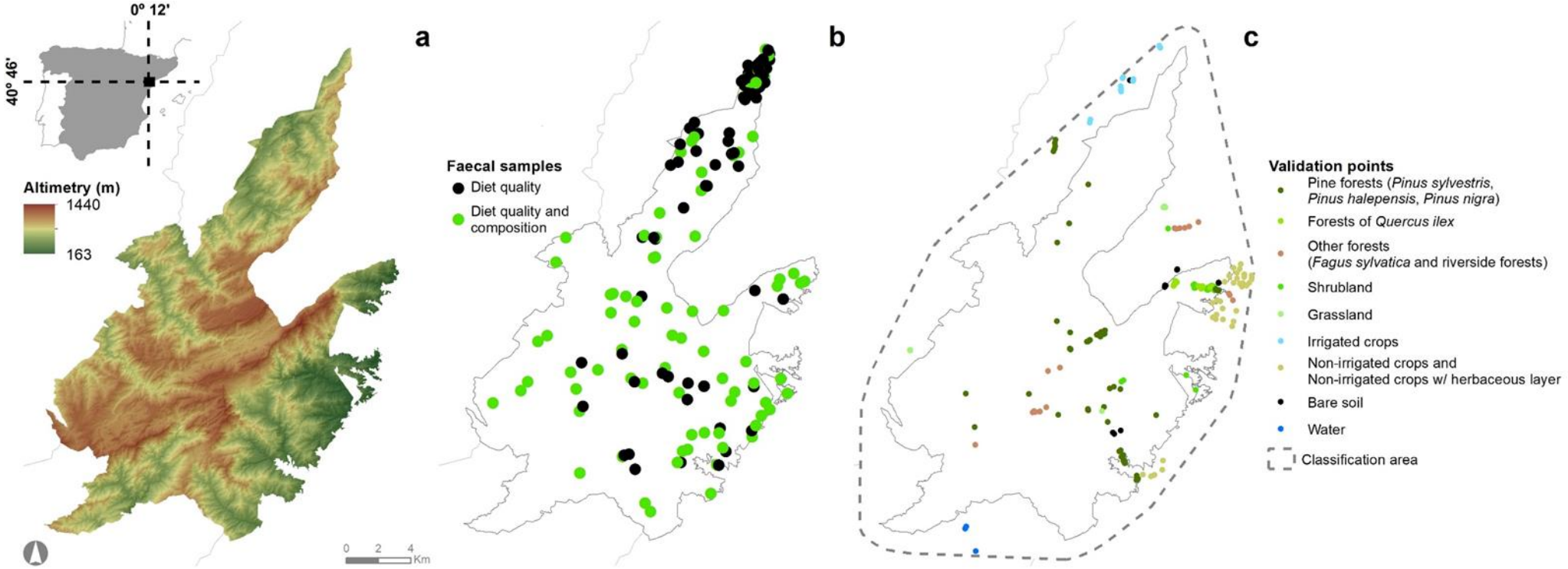

Figure 6. Location of the study area, the *Els Ports de Tortosa i Beseit* National Game Reserve (northeastern Spain, **a**), with the spatial distribution of fecal samples **(b)** and validation/control points **(c)**.

2.2.5. Statistical analysis

We calculated the overall accuracy (OA), the producer's accuracy (PA), the user's accuracy (UA) and the Kappa statistics to assess the reliability of land cover classification. OA is computed by dividing the total number of correctly classified control points by the total number of control points. PA or omission error results from dividing the number of correctly classified control points in each category by the number of reference control points known to belong to that category. UA or commission error is computed by dividing the number of correctly classified control points in each category by the total number of control points that were classified in that category. Kappa statistics compares OA with an expected accuracy.

The seasonal differences in diet quality and composition were assessed using an analysis of variance (ANOVA). Plant species were pooled into four groups: non-leguminous woody (NLWS), leguminous woody (LWS), forbs (Forb) and graminoids (Gram). Fecal samples were grouped in three seasons: spring (21st March – 20th June), summer-autumn (21st June – 20th December) and winter (21st December – 20th March). Summer and autumn samples were pooled into a single category (summer-autumn) because the number of samples collected during the summer was low (n = 8) and the samples were collected at the end of this season. Linear models were used to explore how diet quality varies as a function of diet composition. Data exploration was carried out before the analysis to avoid violating statistical assumptions. Variables were transformed whenever necessary to respect the condition of normality.

Partial least square regressions (PLSR) were applied to assess the relationships between dietary features, vegetation productivity and habitat structure. PLSR analyses the linear combinations among variables and is characterized by their flexibility to handle multicollinear data (Carrascal *et al*., 2009). A PLSR model was fitted for each combination of season and nutritional indicator. The Stone-Geisser Q^2 test was used to assess the significance of PLSR models, whereas their explanatory performance was evaluated by the proportion of variation explained (R^2).

PLSR models were developed using the package "*plspm*" version 0.4.9 (Sanchez *et al*., 2015). All statistical analyses were performed using the statistical software *R* 3.3.0 (R Development Core Team, 2016).

2.3. Results

2.3.1. Diet quality and composition

Throughout the whole study period and considering the analysis of 189 fecal samples, the amount of FN varied between 1.5 and 3.7% (average ± SE: 2.2 ± 0.5%), while the NDF content varied between 24.0 and 60.1% (average ± SE: 49.0 ± 5.9%), the ADF varied between 15.1 and 44.3% (average ± SE: 36.0 ± 4.4%) and the lignin varied between 6.3 and 24.0% (average ± SE: 16.2 ± 2.9%). We detected significant seasonal differences for all diet quality components (**Figure 7**). FN picked during the spring (F = 30.64, P < 0.001), while the peak of fibers fraction was recorded during the winter (NDF: F = 18.33, P < 0.001 and ADF: F = 16.14, P < 0.001).

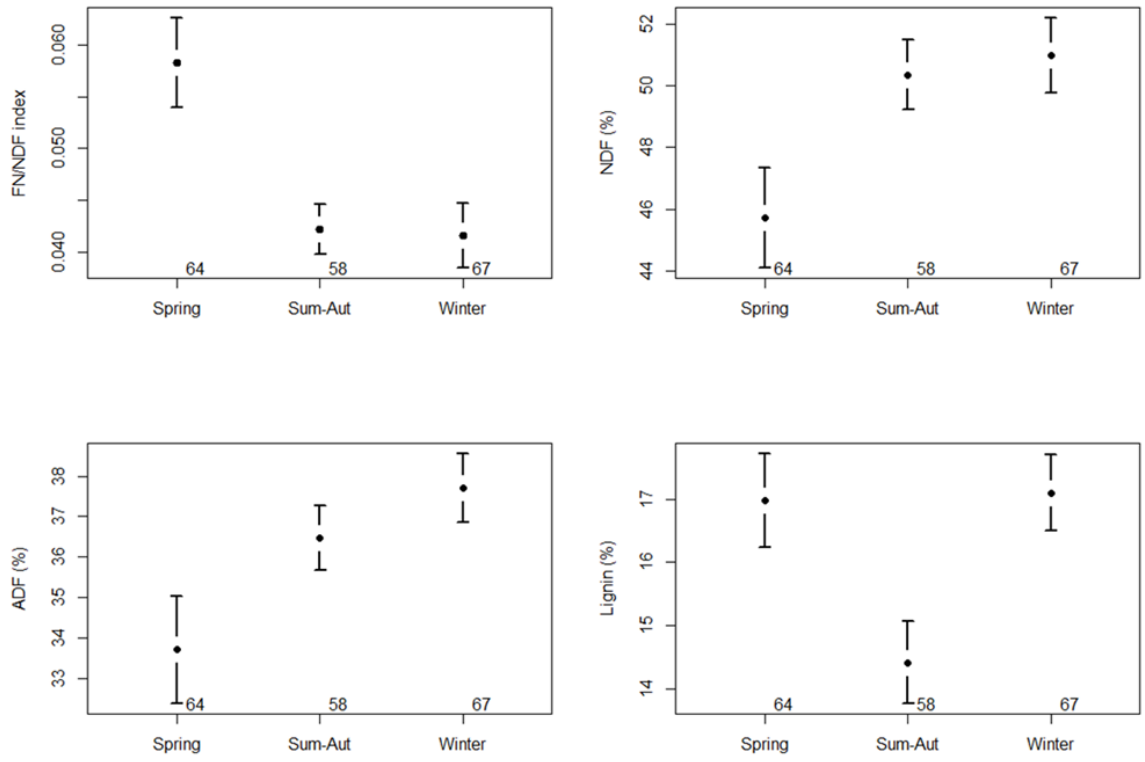

Figure 7. Seasonal patterns in the diet quality of male ibexes. A total of 189 fecal samples were used in the analysis.

The microhistological analysis of 97 fecal samples allowed the identification of 43 plant taxa, of which 63% were identified at species level, 33% at genus level and 4% at family level (**Table 3**). The holm oak (*Quercus ilex*) was the most representative plant species in ibex diet (8,1%), followed by three chamaephytes (*Thymus vulgaris*, *Cistus* sp. and *Rosmarinus officinalis*), and two graminoids (*Brachypodium* sp. and *Festuca* sp.). These species accounted for 37.2% of all fragments analyzed. The representativeness of 25 (approx. 60%) of plant taxa was lower than 1%. Overall, the non-leguminous woody species were the most consumed items over the year (64%), followed by forbs (17%), graminoids (11%) and leguminous woody species (8%). We detected seasonal patterns in ibex diet. We showed that diet composition followed a seasonal trend for non-leguminous woody species (F = 5.13, P < 0.05), forbs (F = 3.53, P < 0.05) and leguminous woody species (F = 3.54, P < 0.05). The consumption of non-leguminous woody species increased during the winter, while leguminous woody species and forbs were more representative in the spring (**Figure 8**). No trend was recorded for graminoids (F = 0.40, P = 0.67).

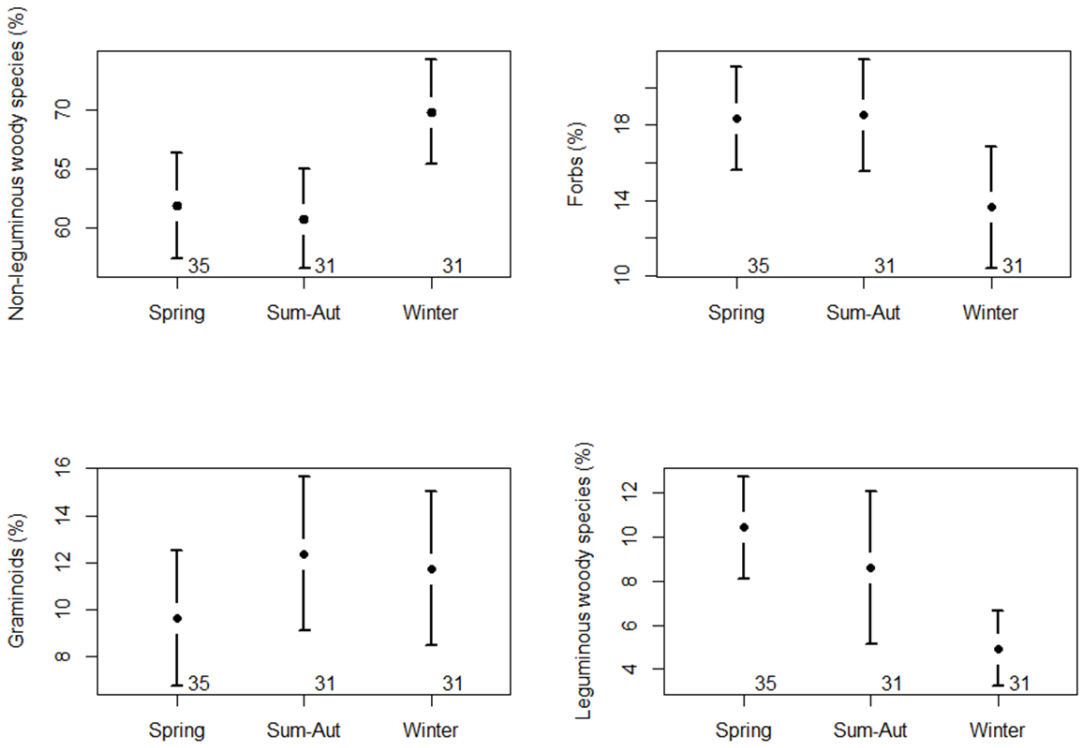

Figure 8. Seasonal patterns in the diet composition of male ibexes. The analysis was based on 97 fecal samples evenly distributed throughout the study area.

Table 3. Diet composition of male ibexes inhabiting the *Els Ports de Tortosa i Beseit* National Game Reserve. Values refer to the total and seasonal proportion of each plant species in male ibexes' diet. These values were calculated considering the total number of fragments (n = 200) observed in each fecal sample. Values between brackets refer to the minimum and maximum proportion.

Group	Species	Total (%)	Spring (%)	Summer/Autumn (%)	Winter (%)
Non-leguminous woody species	*Quercus ilex*	8.1 (5.9 - 10.2)	3.2 (0.9 - 5.5)	8.7 (1 - 16.5)	10.2 (7.3 - 13.2)
	Other species	7.9 (7 - 8.8)	6.6 (5.2 - 8.1)	9.3 (6.8 - 11.9)	8.2 (6.9 - 9.5)
	Thymus vulgaris	7.8 (5.8 - 9.8)	10.4 (6 - 14.8)	3.1 (1.7 - 4.4)	7.6 (5.1 - 10.1)
	Cistus sp.	6.9 (5.6 - 8.1)	10.9 (8.4 - 13.4)	7.5 (3.9 - 11.1)	4.9 (3.5 - 6.2)
	Rosmarinus officinalis	6.7 (5.4 - 8)	4.9 (2.7 - 7.1)	1.9 (0.2 - 3.6)	8.5 (6.8 - 10.2)
	Pinus sp.	3.4 (2.1 - 4.7)	2.2 (0.8 - 3.5)	5.5 (0.6 - 10.5)	3.6 (1.8 - 5.4)
	Hedera helix	3.3 (1.8 - 4.7)	4.4 (0.7 - 8.1)	5.6 (2 - 9.3)	2.3 (0.8 - 3.8)
	Pistacea lentiscus	3.1 (2.2 - 4)	1.6 (0.8 - 2.3)	3 (1.1 - 4.9)	3.8 (2.4 - 5.3)
	Satureja montana	3.1 (2.1 - 4.1)	5.6 (2.8 - 8.5)	3.8 (1.7 - 5.9)	1.8 (1.1 - 2.4)
	Erica multiflora	3 (2.2 - 3.7)	1.9 (1 - 2.9)	2.7 (0.3 - 5)	3.5 (2.4 - 4.5)
	Quercus coccifera	2.3 (1.3 - 3.4)	0.6 (0.2 - 1)	0.9 (0 - 2.4)	3.4 (1.8 - 5.1)
	Juniperus sp.	1.5 (1.1 - 2)	1.1 (0.4 - 1.8)	0.5 (0 - 0.9)	2 (1.3 - 2.7)
	Rubus ulmifolius	1.5 (0.8 - 2.1)	3.1 (1.1 - 5)	1.3 (0 - 2.9)	0.8 (0.4 - 1.2)
	Olea europaea	1.1 (0.4 - 1.8)	0.4 (0 - 1.2)	1.6 (0 - 3.9)	1.3 (0.2 - 2.3)
	Phillyrea latifolia	0.9 (0.4 - 1.4)	1.2 (0.1 - 2.3)	0.7 (0 - 2)	0.8 (0.1 - 1.4)
	Buxus sempervirens	0.8 (0.4 - 1.3)	0.2 (0 - 0.4)	0.3 (0 - 0.7)	1.2 (0.5 - 2)
	Crataegus monogina	0.8 (0.4 - 1.1)	0.4 (0.1 - 0.7)	1.2 (0 - 2.6)	0.9 (0.4 - 1.3)
	Smilax aspera	0.6 (0.2 - 1)	0.2 (0 - 0.3)	3.4 (0.8 - 6)	0.2 (0 - 0.5)
	Prunus spinosa	0.2 (0.1 - 0.3)	0.1 (0 - 0.2)	0.4 (0 - 0.9)	0.2 (0 - 0.4)
	Prunus sp.	0.2 (0 - 0.6)	0.7 (0 - 1.9)	0.2 (0 - 0.7)	0
	Inula viscosa	0.2 (0 - 0.3)	0.1 (0 - 0.3)	0.6 (0 - 1.3)	0.1 (0 - 0.2)
	Rhamnus alaternus	0.2 (0 - 0.3)	0.2 (0 - 0.5)	0.1 (0 - 0.2)	0.1 (0 - 0.3)
	Helianthemum sp.	0.1 (0 - 0.2)	0.1 (0 - 0.1)	0	0.2 (0 - 0.3)
	Lonicera	0.1 (0 - 0.2)	0.1 (0 - 0.4)	0	0.1 (0 - 0.3)

	xylosteum				
	Rosa sp.	0.1 (0 - 0.2)	0	0	0.1 (0 - 0.3)
	Viburnum thymus	0.1 (0 - 0.2)	0	0	0.1 (0 - 0.3)
	Arbutus unedo	0.05 (0 - 0.1)	0.1 (0 - 0.2)	0.04 (0 - 0.1)	0.04 (0 - 0.1)
	Chamaerops humilis	0.04 (0 - 0.1)	0	0	0.1 (0 - 0.1)
Forb species	Other species	9.1 (8 - 10.2)	9.1 (6.9 - 11.3)	9.6 (7.7 - 11.6)	9 (7.5 - 10.5)
	Lamiaceae/*Asteraceae*	6.7 (5 - 8.4)	7.7 (4.6 - 10.8)	8.4 (3.8 - 6.6)	5.7 (3.6 - 7.8)
	Capsella bursa-pastoris	0.8 (0.3 - 1.2)	1.5 (0.2 - 2.8)	0.8 (0 - 1.8)	0.4 (0 - 0.8)
	Verbascum sp.	0.2 (0.1 - 0.3)	0.3 (0 - 0.6)	0	0.2 (0 - 0.3)
	Rubia peregrina	0.1 (0 - 0.2)	0.1 (0 - 0.2)	0.5 (0 - 1.2)	0.1 (0 - 0.2)
	Iridiaceae/*Orchidaceae*	0.02 (0 - 0.1)	0.1 (0 - 0.2)	0	0
Graminoid species	*Brachypodium* sp.	3.9 (2.8 - 4.9)	3.4 (1.7 - 5.1)	3.1 (0.5 - 5.6)	4.3 (2.8 - 5.7)
	Festuca sp.	3.8 (2.8 - 4.7)	3.2 (1.5 - 5)	3.3 (2 - 4.7)	4.1 (2.8 - 5.4)
	Other species	2.3 (1.8 - 2.8)	2.8 (1.5 - 4.1)	2.3 (1.5 - 3.1)	2 (1.5 - 2.6)
	Carex sp.	0.9 (0.6 - 1.2)	0.7 (0.1 - 1.3)	1.2 (0.2 - 2.1)	0.9 (0.6 - 1.3)
	Poa sp.	0.2 (0.1 - 0.4)	0.3 (0.1 - 0.5)	0.3 (0 - 0.8)	0.2 (0 - 0.4)
	Arrhenatherum bulbosum	0.1 (0 - 0.2)	0.1 (0 - 0.3)	0.2 (0 - 0.4)	0.1 (0 - 0.2)
Leguminous woody species	Other species	4 (3.1 - 5)	5.7 (3.7 - 7.8)	4.1 (1.8 - 6.4)	3.2 (2 - 4.4)
	Dorycnium sp.	1.6 (0.8 - 2.4)	1.6 (0.5 - 2.8)	3.2 (0 - 7.5)	1.2 (0.4 - 2.1)
	Genista pilosa	1.5 (0.9 - 2.1)	2 (0.7 - 3.2)	0.5 (0 - 1)	1.5 (0.8 - 2.3)
	Coronilla sp.	0.8 (0.4 - 1.2)	0.7 (0 - 1.5)	0 (0 - 0.1)	1 (0.4 - 1.6)
	Cytisus sp.	0.1 (0 - 0.1)	0.02 (0 - 0.1)	0.2 (0 - 0.6)	0.05 (0 - 0.1)
	Ononis spinosa	0.1 (0 - 0.1)	0.2 (0 - 0.3)	0	0.05 (0 - 0.1)
	Ulex parviflorus	0.02 (0 - 0.1)	0	0	0.04 (0 - 0.1)

Our results corroborate our first hypothesis, *i.e*. the nutritional condition of ibexes is related with diet composition. However, seasonality shapes this relationship (**Figure 9**). Diets rich in non-leguminous woody species were nutritionally poor during the summer-autumn period (β = -0.0002, SE = 0.0001, t = -1.863, P < 0.1). High-quality diets were positively and significantly related with the percentage of forbs ingested during the summer-autumn (β = 0.0006, SE = 0.0002, t = 3.837, P < 0.001) and winter (β = 0.0007, SE = 0.0002, t = 2.918, P < 0.05) periods. Surprisingly, this trend was reversed in the spring. No

significant evidences were observed for the relationship between diet quality and the amount of graminoids and leguminous woody species ingested.

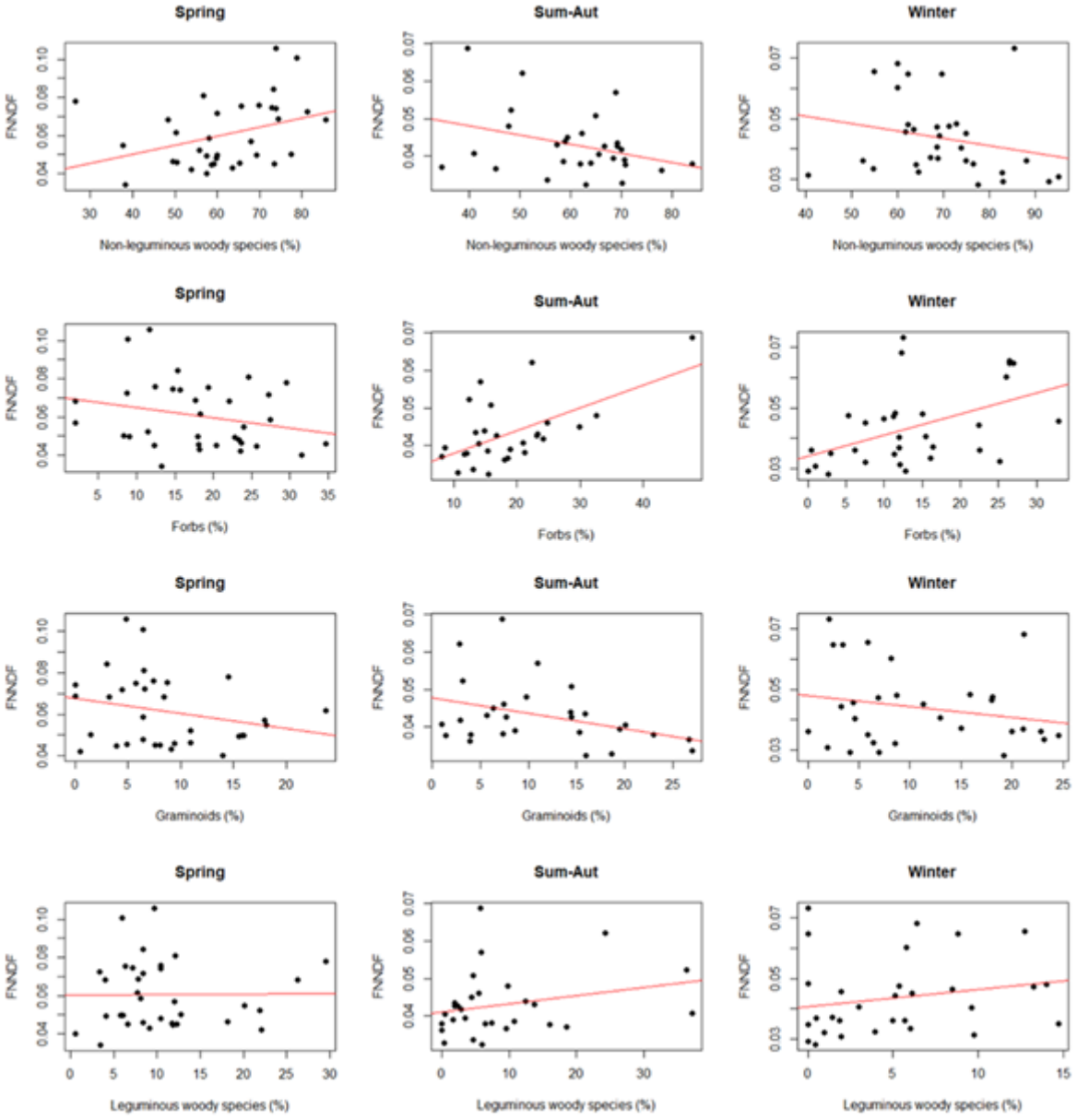

Figure 9. Seasonal relationship between diet quality, here expressed as the ratio between fecal nitrogen and neutral detergent fiber, and diet composition of male ibexes.

2.3.2. Nutritional indicators, vegetation productivity and habitat structure

The OA of land cover classification recorded a high value (0.73) and the Kappa statistics reveals a good agreement between the classification and the training dataset (0.76). Detailed results regarding the accuracy of land cover classification are presented in the **table 4**.

Table 4. Statistical assessment of land cover classification accuracy. The columns represent the reference categories, whereas rows represent the categories deduced from the classification. Diagonal values represent the number of points correctly classified and the marginal values indicate allocation errors. A – Irrigated crops. B – Water. C – *Fagus sylvatica* forest. D – Non-Irrigated crops. E – Scrubland. F – *Pinus nigra* forest. G – Riverside woodland. H – Grassland. I – Non-irrigated crops with herb layer. J - *Pinus halepensis* forest. K – Bare soil. L – *Quercus ilex* forest. M – *Pinus sylvestris* forest.

		Training dataset														
		A	B	C	D	E	F	G	H	I	J	K	L	M	Total	UA
Classification data	A	10	0	1	0	1	0	0	0	0	0	0	0	0	12	0.83
	B	0	3	0	0	0	0	0	0	0	0	0	0	0	3	1.00
	C	0	0	6	0	0	0	0	0	0	0	0	0	0	6	1.00
	D	0	0	0	17	0	0	0	0	0	0	0	0	0	17	1.00
	E	0	0	0	0	21	0	0	0	0	1	0	1	0	23	0.91
	F	0	0	0	0	0	8	0	0	0	1	0	4	2	15	0.53
	G	2	0	1	0	5	0	9	0	0	0	0	6	0	23	0.39
	H	0	0	0	0	5	0	0	7	1	0	0	0	0	13	0.54
	I	0	0	0	3	0	0	0	0	12	2	0	0	0	17	0.71
	J	0	0	0	0	0	1	0	0	0	23	0	1	6	31	0.74
	K	0	0	1	2	0	2	0	2	0	1	17	0	0	25	0.68
	L	0	0	0	0	0	0	0	0	0	0	0	16	0	16	1.00
	M	0	0	0	0	0	8	0	0	0	0	0	0	15	23	0.65
	Total	12	3	9	22	32	19	9	9	13	28	17	28	23		
	PA	0.83	1.00	0.67	0.77	0.66	0.42	1.00	0.78	0.92	0.82	1.00	0.57	0.65		

As diet quality and composition varied over the year, the relationship between dietary features, vegetation productivity and habitat structure were analyzed by season. During the spring, the explanatory component of PLSR analyses explained 18.42% of the observed variability of ibex diet. In the summer-autumn and winter, this component explained 21.27% and 25.54% of the observed variability, respectively. We reported different signs between loads

of the explanatory and response components. During the spring, we recorded a positive relationship between NDVI and FN concentrations ($Load_{NDVI}$ = 0.91; $Weight_{NDVI}$ = 0.93; $Load_{FN}$= 0.22) and a negative relationship between NDVI and the amount of NDF ($Load_{NDF}$ = -0.27). The positive relationship between NDVI and FN concentrations is kept during the summer-autumn ($Load_{NDVI}$ = 0.51; $Weight_{NDVI}$ = 0.46; $Load_{FN}$= 0.28), but is reversed in the winter ($Load_{NDVI}$ = -0.30; $Weight_{NDVI}$ = -0.29; $Load_{FN}$= 0.23). We found that the representativeness of shrubs and natural pastures is positively associated with high-quality diets and low-fibers. This relationship is particularly evident in the spring ($Load_{shrubs}$ = 0.53; $Weight_{shrubs}$ = 0.51; $Load_{natural\ pastures}$ = 0.69; $Weight_{natural\ pastures}$ = 0.69; $Load_{FN}$ = 0.22; $Load_{NDF}$ = -0.27; **Figure 10**). No relationship between habitat structure and diet quality was reported for summer-autumn and winter. We observed an erratic relationship between diet composition, vegetation productivity and habitat structure. The Stone-Geisser Q^2 demonstrated that the association between explanatory and response components, encompassing all variables of diet composition, vegetation productivity and habitat structure, was not significant.

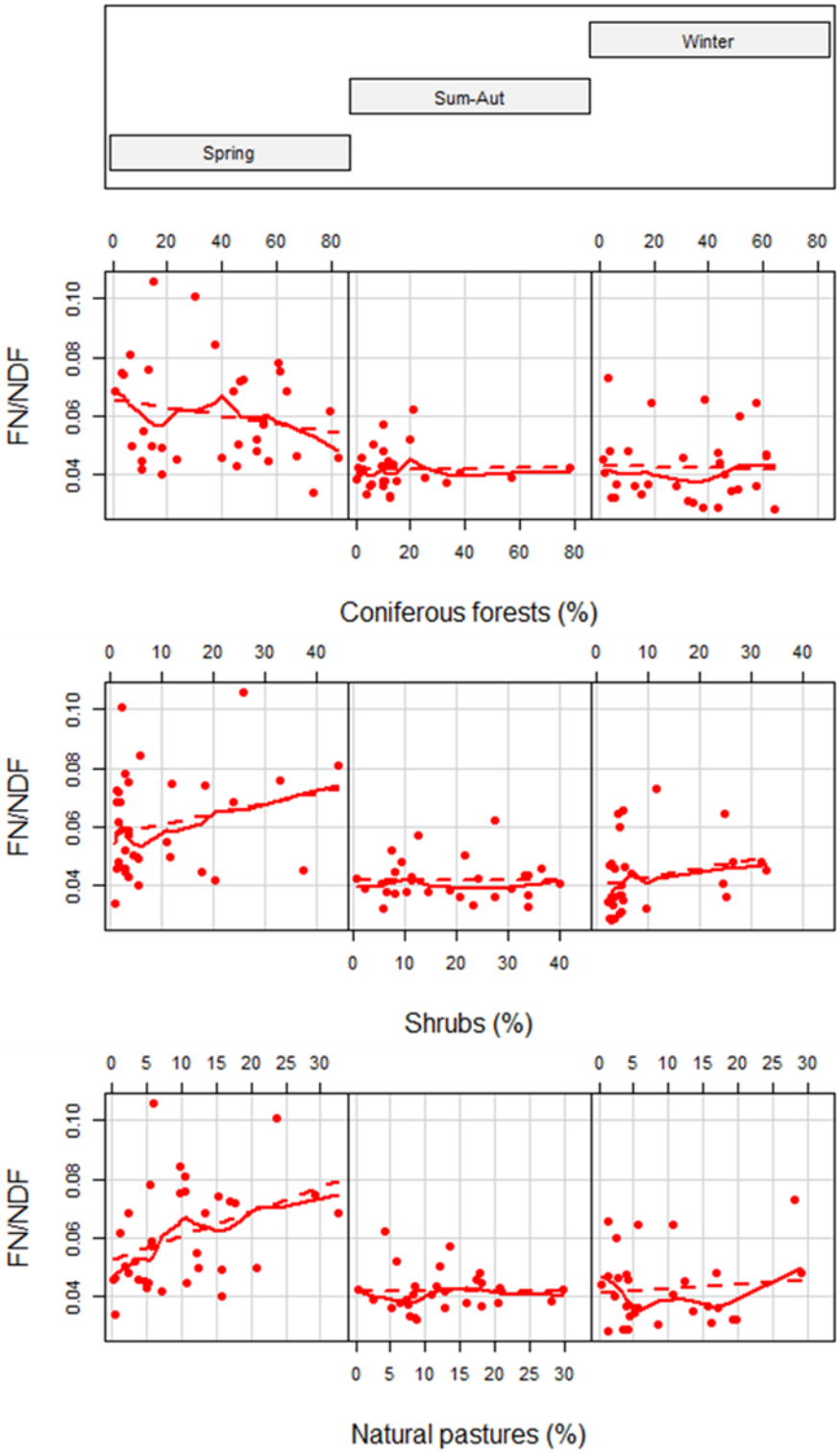

Figure 10. Seasonal relationship between diet quality, here expressed as the ratio between fecal nitrogen and neutral detergent fiber, and the percentage of coniferous forests, shrubs and natural pastures within an area of 550 hectares centered at fecal sample location.

2.4. Discussion

The number of studies using satellite-derived products to link vegetation productivity and habitat characteristics to population dynamics and life-history traits of wild species is increasing (Trimble *et al*., 2009; Hurley *et al*., 2014). However, few were able to validate the functional relationship between remote-sensed metrics, changes in vegetation quality and the dietary features of wild ungulates. Here, by using fecal indicators as an alternative to direct forage surveys (Ryan *et al*., 2012), we show that seasonality drives the diet quality and composition of wild ibexes (Hypothesis 1), modulates the interaction between these two nutritional indicators (Hypothesis 2) and shapes the relationship between dietary features, vegetation productivity and habitat structure (Hypothesis 3).

2.4.1. Seasonal patterns in diet quality and composition

The feeding behavior of Iberian ibex varies seasonally (Martínez, 1985), altitudinally (Martínez, 2000) and geographically (Acevedo & Cassinello, 2009). We observed that the amount of fecal nitrogen decreased from the spring to winter, while the amount of fibers and lignin followed an opposite trend. This negative relationship was in line with our expectations, as forage digestibility is reduced by higher fibre content (Van Soest, 1994). Surprisingly, the seasonality of our results contrasts with previous studies carried out in other Mediterranean areas (red deer *Cervus elaphus*, Miranda *et a*l., 2012; Santos *et al*., 2018), but agree with the results reported for wild ungulate populations inhabiting highly seasonal mountain habitats (Pyrenean chamois *Rupicapra pyrenaica pyrenaica*, Gálvez-Cerón *et al*., 2013). The closer example come from Sierra Nevada, where a nine-year study on Iberian ibex body condition, showed that individual body stores were highest during the spring/summer (*i.e*. high body condition, high-quality diets) (Serrano *et al*., 2011; see also Martínez, 2000).

We showed that browsing predominates in PTB, which agrees with a previous study performed 25 years ago in the same area (Martínez, 1994). Both studies recorded significant seasonal differences in diet composition and

demonstrated that woody plants were the most consumed food item all year around. This result supports our first hypothesis. Woody species (*e.g. Quercus ilex* and *Phillyrea latifolia*), were also the main food component of Iberian ibex diet in Sierras de Cazorla and Segura, a Mediterranean ecosystem located in southern Spain (Martínez, 1985). A distinctive feature of our study indicated, however, that the consumption of non-leguminous woody plants remains high even during the spring (> 60%), and that the representativeness of forbs and graminoids on ibexes' spring diet was reduced by 10-15% in relation to Martínez (1994). The pervasive and ongoing conversion of natural pastures and open meadows into dense pinewoods in PTB supports these differences.

The relationship between diet quality and composition during the spring contrary our expectations, as the fecal nitrogen increases with the percentage of non-leguminous woody species and is inversely related with the percentage of forbs. Though it may seem surprising, this result may have multiple and non-exclusive explanations. First, the physical characteristics of Mediterranean mountainous habitats, such as PTB, results in small-scale differences regarding phenology, growth, biomass and nutritious value of plant species (Albon & Langvatn, 1992, Duparc *et al*., 2013). For instance, Schweiger *et al*., (2015) showed that plant nutrient content is very variable within vegetation communities and Reed & McCarthy (1996) demonstrated that slope and aspect influence the chemical properties of plants. Second, plant nitrogen content might not directly reflect the quality of forage (Codron *et al*., 2007). The amount of fecal nitrogen excreted is influenced by plant secondary metabolites, such as tannins. Condensed tannins bind to protein and avoid protein degradation in the rumen, increasing nitrogen retention and absorption (Lamy *et al*., 2011). Plants rich in tannins are particularly sought by goats during the spring and summer periods due to their anti-helminthic effects (Min & Hart, 2003). Therefore, small-scale and seasonal differences in tannin content may confound the expected relationship between diet quality and composition. Finally, diet analysis was only based on male ibexes. As nutritional requirements vary with sex (Clutton-Brock *et al*., 1987; Ruckstuhl & Neuhaus, 2000), we hypothesize that foraging efficiency during the spring is more important for females, which have to nourish their offspring. Males are more flexible in their dietary choices, and their space use are not so influenced by forage quality (nutritional needs hypothesis,

Demment & Van Soest, 1985; see also the Jarman–Bell principle, Bell, 1971; Jarman, 1974). Here, we reported a positive and significant relationship between spring FNNDF and the percentage of natural pastures within the ibex home range. One explanation for the apparent contradiction between this result and the negative relationship between FNNDF and the percentage of forbs could be the scale of analysis and the heterogeneity of Mediterranean habitats.

2.4.2. Relationship between nutritional indicators and remotely-sensed indexes

From an ecological and methodological perspective, our results have important implications at one major respect. Even though NDVI proved its usefulness in assessing and predicting forage quality and availability in alpine, savanna and forest habitats (Hamel *et al*., 2009; Ryan *et al*., 2012; Borowik *et al*., 2013), our study showed that the direct link between satellite products (*e.g*. NDVI) and diet quality of wild ungulates inhabiting highly heterogeneous habitats must be done with caution. We pointed three possible explanations that support the lack of a significant relationship between NDVI and diet quality. First, our study area is characterized by abundant bare ground and patchy habitats of woods, shrub, herbaceous and sparse vegetation. These landscape features may lead to differences in the spectral response of plants and to inaccurate estimates of plant productivity (Huete *et al*., 1985). Second, the spectral response of tree canopy does not reflect the quality and availability of understory and accessible vegetation (see also Borowik *et al*., 2013). Third, the feeding behavior of ibexes is likely to be more influenced by resource availability than by vegetation quality (Martínez, 2000). Finally, NDVI was used at the scale of 500 m x 500 m. We do not exclude the possibility that ibexes select food resources at reduced scales (Schweiger *et al*., 2015). For example, it was demonstrated that fecal crude protein of alpine ungulate populations is better predicted by small-scale NDVI than by large-scale data (Hamel *et al*., 2009; see also Schweiger *et al*., 2014). We advocate that can be counterproductive up-scale our results to a regional extent, as the relationships we explored may be context-dependent and may vary with the target species

(Schweiger *et al*., 2014). For instance, our results did not match the findings of a large-scale study on the dietary quality and nutritional condition of Mediterranean red deer populations (Santos *et al*., 2018), where it was reported that fecal nitrogen is affected significantly and positively by the NDVI.

Here, we analyzed fecal samples as an alternative to vegetation assessments. As stated by Ryan *et al*. (2012), fecal samples are easily acquired and processed, less expensive than vegetation analysis and directly reflect the feeding behavior and dietary choices of species. We are aware, however, that this approach can attract criticism because it is not spatially explicit and, therefore, can make managing decisions imprecise (Mutanga & Skidmore, 2004). Future research should focus on fill this gap, either collecting field data covering a continuous range of vegetation productivity and plant species composition, and using imaging spectroscopy with fine spatial and spectral resolution. This will allow us to discriminate plant species in different growth stages, calculate plant biomass (Cho & Skidmore, 2009), assess the biochemical composition of plant species (Skidmore *et al*., 2010), link nutritional requirements to resources availability and quality (Schweiger *et al*., 2015), parametrize resource maps (Nelson *et al*., 2013), and thus estimate the carrying capacity of Mediterranean habitats. Although hard to achieve, this is an important step toward the understanding of population dynamics of Mediterranean ungulates.

CHAPTER 3 Evidence for phenotypic plasticity but not for compensatory horn growth in male Iberian ibex

* A group of male ibexes roaming a mountain ecosystem. Photo: João Carvalho.

Abstract

The description of horn growth patterns is of utmost importance for the sustainable management of wild ungulate populations subjected to intense trophy hunting. This is a topic of renewed interest because horn growth patterns seem to be contingent on region and population.

We sampled 2,145 male Iberian ibexes (*Capra pyrenaica*) evenly distributed across the *Els Ports de Tortosa i Beseit* National Hunting Reserve, NE Spain. A total of 24,615 annual horn growth segments were measured and used to describe horn growth patterns of male ibexes and to test whether compensatory horn growth occurs in a heterogeneous area.

We found that individual heterogeneity explained more than a quarter (27.75%) of the variability in annual segment length and that habitat characteristics foster significant phenotypic differences among male ibexes. Our results corroborate previous studies by demonstrating that compensatory horn growth in male ibexes, as in other members of the tribe Caprini, is inexistent. Our study goes one step further and suggests that compensatory horn growth in male ibexes is neither promoted by cohort effects nor by habitat differences.

The absence of compensatory horn growth has important management implications, namely: (i) male ibexes are not able to recover from a bad start, and (ii) the species is prone to evolutionary effects from trophy hunting. We emphasize that the study of just one proxy of horn growth may hamper the current knowledge about compensatory mechanisms in wild ungulates and imperil the development of effective management measures.

Keywords *Capra pyrenaica*, game management, habitat, horn growth patterns, phenotypic plasticity, population management, size-selective harvesting, trophy hunting

3.1. Introduction

Horns are permanent epidermal structures whose size and shape contribute to establish dominance hierarchies amongst males of polygynous species (Geist, 1966). In *Caprinae*, horn growth continues throughout the animal's life but the rate to which it occurs varies with season and decreases with advancing age (Bergeron *et al*., 2008). Horn growth is not only driven by intrinsic factors such as age, sex or genetic variability of individuals, but also by the interactions between the individual characteristics and extrinsic variables such as resource availability and harvesting strategies (Monteith *et al*., 2013). Horns are generally considered honest signals of individual health (Ezenwa & Jolles, 2008) and are sometimes expected to provide an indication of habitat quality (Garel *et al*., 2007).

Trophy hunting of ungulate males with large and symmetric horns is widespread and can produce important revenues for game managers and wildlife conservation (Loveridge *et al*., 2006). The selective harvesting of these horn-like structures, too often intensive and unrestrictive, has raised an increasing concern about the evolutionary consequences and ultimately, the socio-economic implications of this activity. Recent studies have shown that trophy hunting causes a significant reduction in horn size and bodyweight on the short-term (Pigeon *et al*., 2016). This is partly because individuals with desirable phenotypes (valuable trophies) are more prone to be removed before they can breed (Coltman *et al*., 2003). Additionally, it may also trigger several demographic consequences such as males reproducing earlier and the consequent destabilization of social structures (Milner *et al*., 2007). Unequivocal evidence moreover shows that changes in observed phenotypic traits may result from a combination of size-selective harvesting and environmental factors (Douhard *et al*., 2017). The horns of bovids stop growing in winter, usually forming a distinct segment (annulus). Because large horns are energetically demanding, environmental variations able to impact forage availability and quality may affect the yearly-horn growth. For instance, it was demonstrated that a decrease in resource availability led to more resources being allocated to body growth than to horn growth in young bighorn rams (*Ovis canadensis*),

possibly increasing short-term survival at the cost of decreased long-term reproductive success (Festa-Bianchet *et al*.,2004).

Compensatory growth is the mechanism whereby an organism compensates the growth depression, resulting from periods of food restriction and nutrients shortage, by increasing the relative resource allocation to a specific trait when environmental and nutritional conditions improved (Jobling, 2010; Metcalfe & Monaghan, 2001). Thereafter, the consequences of trophy hunting and unfavorable environmental conditions are particularly evident in species where compensatory horn growth is weak or absent (Festa-Bianchet, 2016). Empirical evidence suggests that compensatory horn growth may be significant in species where the majority of horn growth occurs at a young age (*e.g*. Mountain goats *Oreamnos americanus*, Côté *et al*., 1998; Alpine chamois *Rupicapra r. rupicapra*, Corlatti *et al*., 2015), but may be weak in species where horn growth occurs at high rates, even in adulthood (*e.g*. Alpine ibex *Capra ibex ibex*, Toïgo *et al*., 1999). Although the species' ability to increase growth rates may mitigate the effects of a bad start, compensatory growth may carry long-term costs, and is often contingent on life stages and specific traits (Metcalfe and Monaghan, 2001). For instance, in species where the development of structural sexual ornaments is an inextricable aspect of reproductive success (*e.g*. horns in *Caprinae* are used in contests for mates), investment in sexual ornaments may lead to reduced individual body size and/or reduced chances of survival (Lindström *et al*., 2005).

As variation in horn size and shape of male *Caprinae* subjected to intensive harvesting regimes, and variable environmental conditions, can have demographic, evolutionary and socio-economic implications, assessing the possibility of compensatory horn growth on those populations is becoming of growing importance for many wildlife managers. This is obviously a subject of concern since the lack of compensatory horn growth typically means that slower-growing young males become small-horned mature males (Toïgo *et al*., 2013). Furthermore, although recent studies did explore the possibility of compensatory growth in *Bovidae* (Alpine ibex: Toïgo *et al*., 1999; Bergeron *et al*., 2008, Toïgo *et al*., 2013; Bighorn rams: Festa-Bianchet *et al*., 2004), the relative importance of habitat characteristics in shaping horn growth remains largely unknown. The Iberian ibex (*Capra pyrenaica*) is the most economically

valuable species in Spain and its management is focused on the production of large-horned males. Trophy hunting of male ibexes is widespread throughout the country and it is based on the overall rank of horn size, horn symmetry and age (Pérez *et al*., 2011a). In the *Els Ports de Tortosa i Beseit* National Hunting Reserve, NE Spain, Iberian ibex males have been trophy-harvested over the last four decades. Individuals of low phenotypic value are also selectively removed in an attempt to reduce the intraspecific competition and to limit the reproduction of undesired phenotypes (Pérez *et al*., 2011a). This harvesting regime has been seen as a management strategy to ensure the long-term sustainability of the hunting activity because it counteracts the undesirable effects of trophy hunting on the distribution of the affected phenotypic trait, the horn size and shape. Although this strategy might be enough to offset the evolutionary consequences of trophy hunting (Mysterud & Bischof, 2010), the lack of knowledge on how environmental conditions may affect horn growth patterns hampers the implementation of spatially explicit countermeasures to alleviate trophy hunting impacts. A better understanding of horn growth patterns would therefore be a most welcome first step towards the effective management of this species. Taking advantage of a long-term monitoring of an Iberian ibex population, we here aim to: (i) explore whether individual heterogeneity, cohort and sampling locations foster well-differentiated horn growth patterns in male ibexes and (ii) assess if compensatory horn growth occurs. Horn growth patterns and phenotypic quality differ sharply between individuals and this difference may be exacerbated by environmental conditions (Alpine ibex, Bergeron *et al*., 2008; thinhorn sheep *Ovis dalli*, Loehr *et al*., 2010). Because horns are energetically costly to produce and carry, we expect marked individual heterogeneities in their expression (Hypothesis 1) and evident plasticity in horn growth patterns between habitats, *i.e*. the correlation between successive horn growth segments is expected to be influenced by the habitat characteristics (Hypothesis 2). Growing evidence from field studies suggests that compensatory horn growth is negligible in tribe Caprini (*e.g*. Toïgo *et al*., 2013; Festa-Bianchet *et al*., 2004), however, the relationship between compensatory horn growth and habitat characteristics remains little explored in species belonging to this prominent tribe (but see Corlatti *et al*., 2015 who explored this relationship in Alpine chamois, tribe Rupicaprini). We here

hypothesize that the large variability in habitat characteristics found in our study area may allow for compensatory horn growth to occur in male ibex inhabiting specific locations (Hypothesis 3).

3.2. Material and methods

3.2.1. Study area

We used accurate measurements of 24,615 annual horn growth segments from 2,145 male ibexes sampled at *Els Ports de Tortosa i Beseit* National Hunting Reserve, north-eastern Spain (PTB, hereafter; 40º48'N, 0º19'E, **Figure 11**). PTB covers an area of 28,587 ha. The landscape is heterogeneous and encompasses a range of Mediterranean-type habitats interspersed by pastures and crops. The substrate is calcareous and the vegetation is mainly composed by Mediterranean forests of *Quercus ilex* and *Pinus halepensis*. The evergreen sclerophyll shrubland characterizes the east part of the study area and harbors the greatest diversity of plant species.

3.2.2. Iberian ibex sampling

All sampled animals were legally and selectively hunted over 18 years (from 1995 to 2013). Sex was determined by visual inspection and age (years) was visually assessed from horn-segment counts (see for details Fandos, 1991). The measurements of annual segments were taken to the nearest mm with a nylon tape measure (horn growth information is not available for 2001, 2002 and 2003). The oldest and outermost annual segment was excluded from our analyses due to abrasion (Álvarez, 1990) and maternal effects (Giacometti *et al*., 2002). Most ibexes had 10–14 growth segments per horn which indicates that they were 11–15 years old when hunted. More than 14 or less than 10 segments per horn were only found in 25% of males.

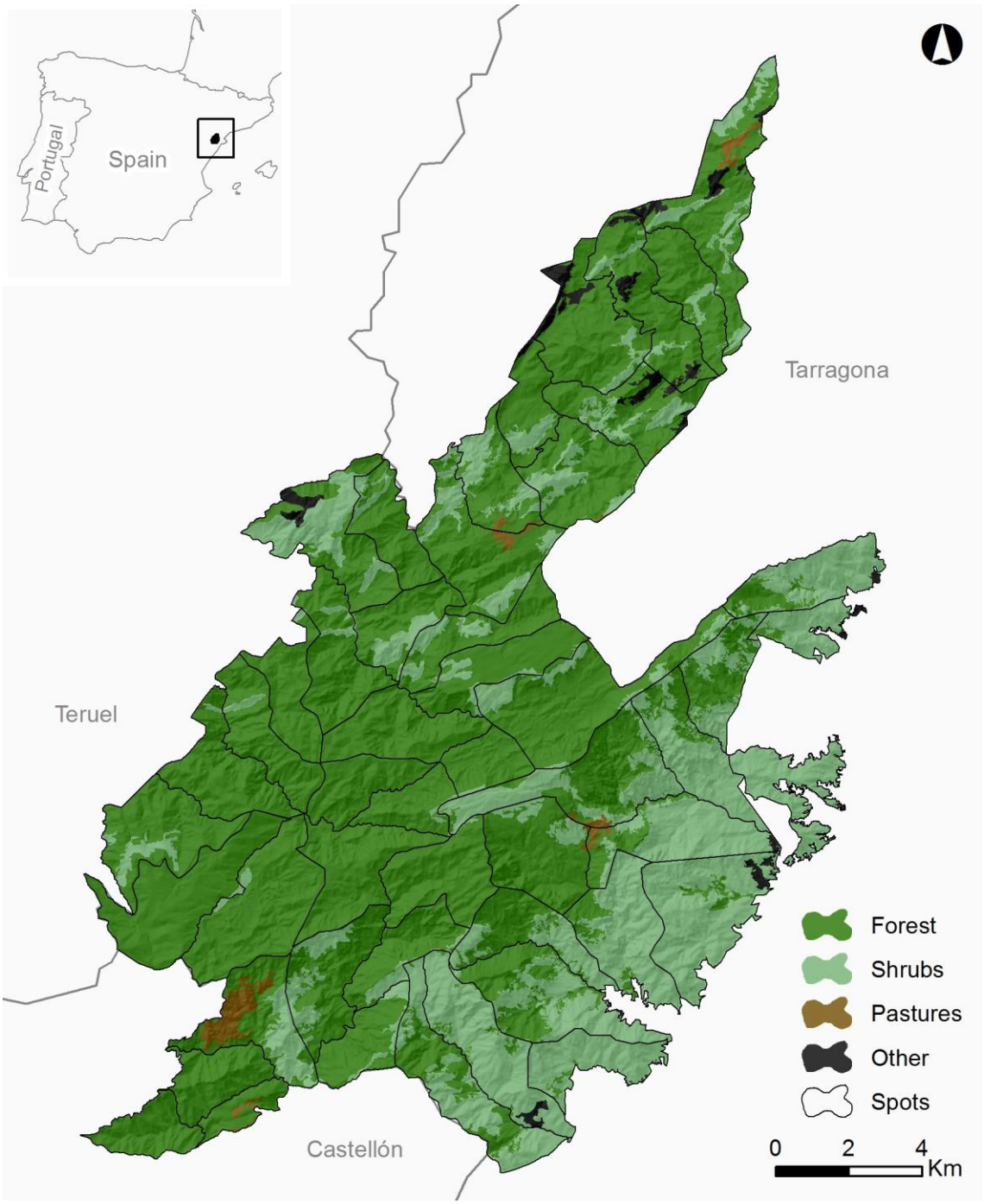

Figure 11. Location of the study area, the *Els Ports de Tortosa i Beseit* National Game Reserve. Main habitat characterization is also presented.

3.2.3. Statistical analyses

By performing a k-means cluster analysis, we identified two distinct clusters that explain 73.11% of the spot variability in terms of habitat characteristics. The first cluster (cluster 1, n = 28 spots) is represented by areas with a great proportion of dense Mediterranean forests (north and west of PTB), while the second cluster (cluster 2, n = 14 spots) is characterized by shrublands interspersed by pasture or agricultural areas (east of PTB). The habitat cluster was used as a fixed factor in the subsequent models. The habitat classification considered the food availability and quality based on the diet of the studied population (Martínez, 1994).

We explored the horn growth patterns as a function of age (years), cohort and habitat cluster using generalized additive mixed models (GAMM). We considered annual segment length (cm) as the response variable, and male identity (ID) as a random factor with varying intercepts and fixed slopes. We fitted ID as a random factor to avoid pseudo-replication and to explore individual heterogeneities in male horn growth. We tested the significance of ID using the likelihood ratio test (LRT, Steele and Hogg, 2003). Out of a total of 50 spots, eight were excluded from the analyses given the low representativeness of male samples (n < 20). We followed the methodological framework adopted in previous studies (Alpine ibex: Toïgo *et al*., 2013; Alpine chamois: Corlatti *et al*., 2015) to explore whether compensatory growth occurred. We performed a regression model between the length of the second segment (log-transformed L2) and the cumulative length of the third, fourth, fifth and sixth segments (log-transformed L3-L6, inflection point; Álvarez, 1990; Sarasa *et al*., 2012). We fitted the cohort and habitat cluster as fixed factors to account for temporal and spatial variability in environmental conditions, respectively. To explore the possibility of fine-scale compensatory growth we ran multiple regressions between subsequent horn growth segments (L3–L2, L4–L3, L5–L4 and L6–L5). Alternative models were compared by applying an information-theoretic approach. The Akaike information criterion (AIC; Akaike, 1974) and the deviance information criterion (DIC; Spiegelhalter *et al*., 2002) were used as the parsimony criteria. A model was selected over another whenever it reduces the AIC in 2 (two) units (Burnham and Anderson, 2002). Statistical significance was

set at $P \leq 0.05$ for all tests. The amount of variation explained by each mixed model (R^2) was calculated following the recommendations of Nakagawa and Schielzeth (2013). The software *R* 3.4.0 (R Development Core Team, 2017) was used to perform the analyses. The "*mgcv*" (Wood, 2012) and the "*gamm4*" (Wood & Scheipl, 2016) packages were used for GAMM analyses and the "*nlme*" package (Pinheiro *et al*., 2012) for linear mixed-effects models.

3.3. Results

Total horn length is driven by the male's age ($\beta = 5.19$, SE = 0.02, $t = 330.30$, $P < 0.0001$, $R^2 = 0.51$, **Figure 12**). Regarding the growth patterns of annual segments, the most parsimonious model included the effects of age, cohort, habitat cluster and the interaction between age and habitat cluster (AIC = 97961.71, DIC = 97867). The second most competitive model only includes the effects of age and habitat cluster, however was at approximately 80 AIC units from the most parsimonious model (AIC = 98041.68, ΔAIC = 79.97, DIC = 98041.68). LRT demonstrated that male identity was highly significant (LRT between the full model and the model without random effect = 702.99, d.f. = 7, $P < 0.001$). Among-individual variations accounted for 27.75% of observed differences in annuli length, confirming our first hypothesis (Hypothesis 1).

As expected, we reported a significant decrease of the annual segment length during adulthood ($\beta = -0.24$, SE = 0.003, $t = -66.38$, $P < 0.001$), particularly evident after the age of eight (**Figure 13**). On the other hand, cohort had no significant effect on the growth patterns of annual segments ($\beta = 0.002$, SE = 0.003, $t = 0.60$, $P = 0.55$). The annual segments of males harvested in shrubland habitats are significantly longer than the segments of males harvested in forest-dominated areas ($\beta = 0.43$, SE = 0.05, $t = 9.23$, $P < 0.001$). This result indicates that male ibexes exhibit substantial phenotypic differences among habitats, confirming our expectations (Hypothesis 2). Male's age and habitat interacted significantly suggesting that the pace of horn growth decreased faster in the shrubland habitats ($\beta = -0.05$, SE = 0.01, $t = -10.13$, $P < 0.001$).

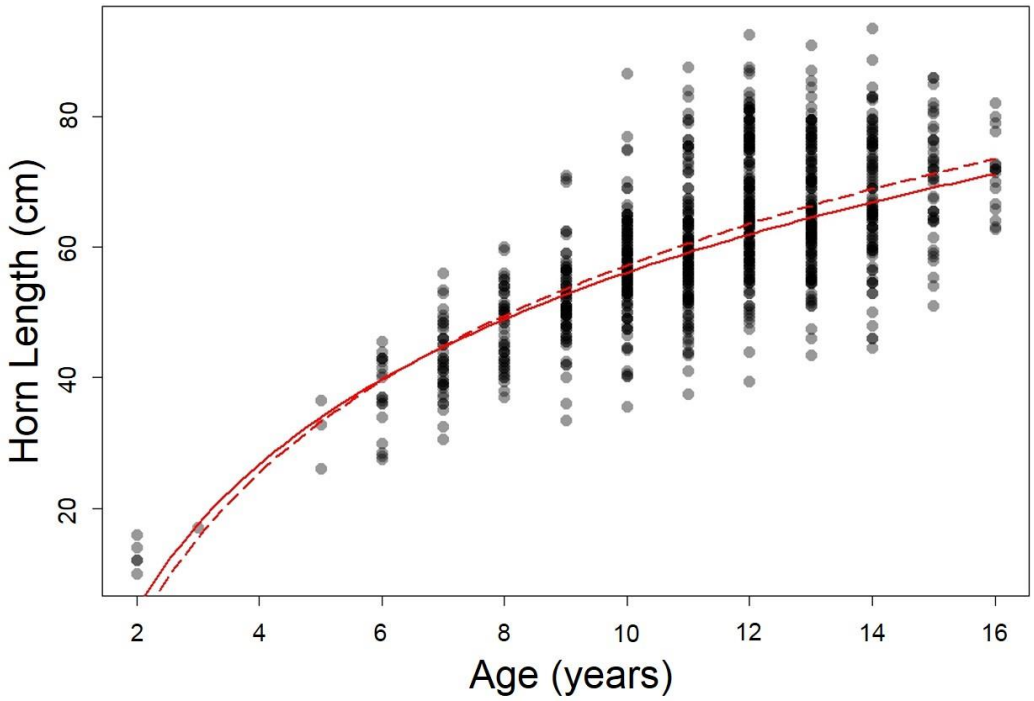

Figure 12. Relationship between total horn length (cm) and age at harvest (years). The red solid line represents the relationship in forest and closure habitats; the red dashed line represents the relationship in shrub- and grass-rich open areas.

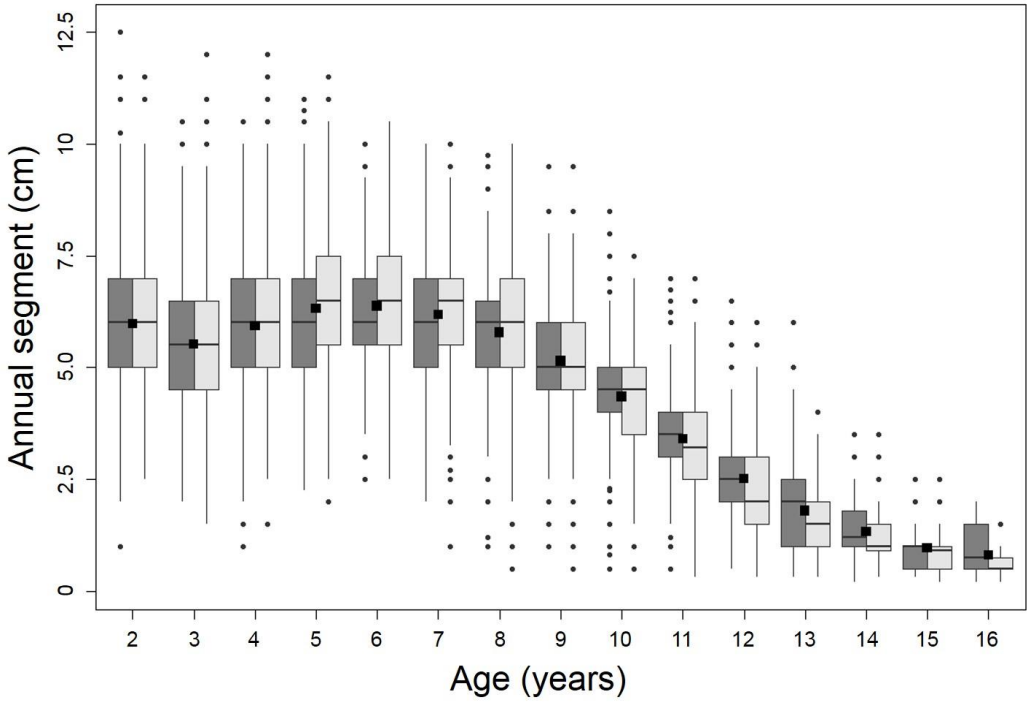

Figure 13. Variation in annual segment length (cm) in relation to age (years) considering forest and closure habitats (dark grey box plots) and shrub- and grass-rich open areas (light grey box plots). Solid black squares represent the overall mean annuli length.

With regards to compensatory horn growth, our results (the length of L2 was positively correlated with the length of L3-L6: β = 0.42, SE = 0.03, t = 13.55, P < 0.001) corroborate the third hypothesis (Hypothesis 3, **Figure 14**), and reinforce the conclusions of previous studies that this mechanism in species belonging to the tribe Caprini is weak or absent. Our results further suggested that neither cohort effects (β = −0.0004, SE = 0.0003, t = −1.31, P = 0.18) nor habitat differences (β = −0.05, SE = 0.06, t = −0.82, P = 0.41) promote the occurrence of this mechanism. The pairwise analyses showed that the length of subsequent annual segments are positively correlated and therefore no evidences for fine-scale compensatory growth were detected (L3–L2: β = 0.42, P < 0.001; L4-L3: β = 0.74, P < 0.001; L5–L4: β = 0.71, P < 0.001; L6–L5: β = 0.64, P < 0.001).

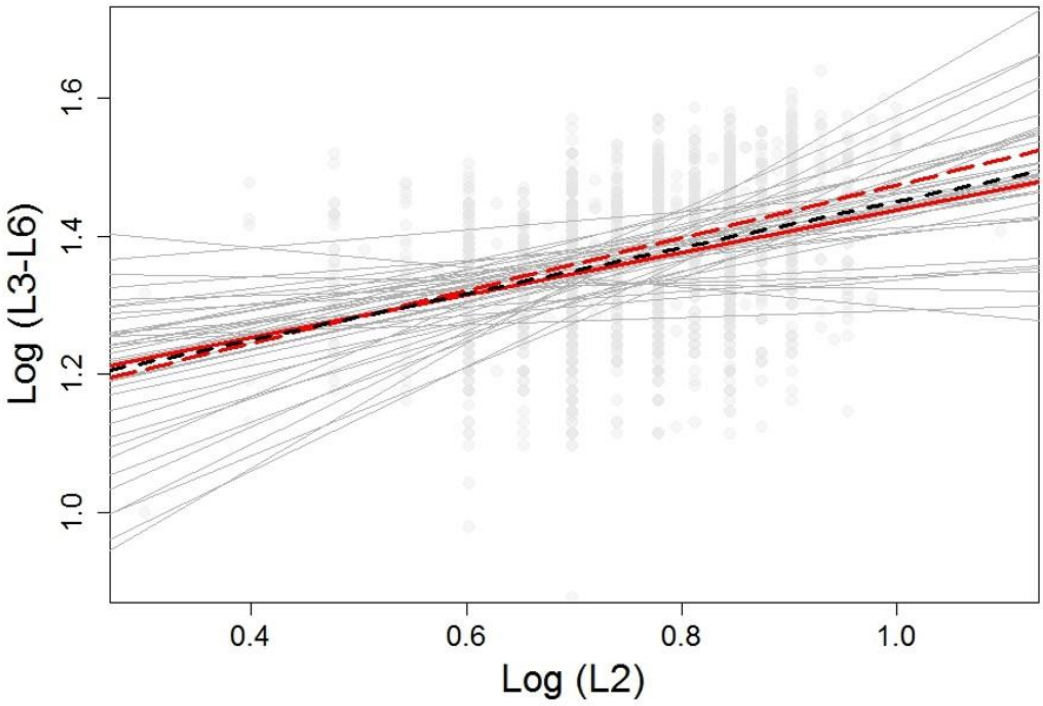

Figure 14. Relationship between log-transformed L2 and log-transformed L3–L6. The black dashed line represents the L2/L3–L6 relationship considering all the sampled males; the red solid line represents the L2/L3–L6 relationship in forest and closure habitats; the red dashed line represents the L2/L3–L6 relationship in shrub- and grass-rich open areas and the grey lines represent the L2/L3–L6 relationship per spot.

3.4. Discussion

The characteristics of our dataset (*e.g*. large number of yearly-horn segments taken from many individuals evenly distributed over the study area) provides an excellent opportunity to explore horn growth patterns and test for compensatory horn growth in male Iberian ibexes. Our results show that individual characteristics lead to well-differentiated horn growth trajectories and provide statistical support for an evident phenotypic plasticity in horn growth, probably due to differences in habitat characteristics and quality of food resources. We reported a positive relationship between L2 and the horn length between the annuli L3-L6, which confirms that compensatory growth of horns length does not occurs in male ibexes, a pattern already described in other studies on ungulates (Alpine ibex: Toïgo *et al*., 1999; Bergeron *et al*., 2008; Toïgo *et al*., 2013; Bighorn rams: Festa-Bianchet *et al*., 2004). Our study goes one step further suggesting that the absence of compensatory horn growth in Iberian ibex does not depend on the cohort or habitat characteristics. The positive correlation between L2 and L3–L6 indicates that L2 could be used as a reliable proxy of horn size at older ages and suggests that males with fast-growing horns early in life will probably become large-horned mature males. The absence of compensatory horn growth may exacerbate individual differences in total horn length among mature males because small-horned young males will not be able to catch-up large-horned young males later in life (Bergeron *et al*., 2008).

Taken as a whole, our findings suggest that variable environmental conditions, here represented by habitat characteristics, experienced throughout life foster well differentiated phenotypes among individuals (Dmitriew, 2011). In fact, individuals born in areas or periods of poor food provisioning tend to exhibit slower growth rates throughout life than those born under favorable conditions (Hamel *et al*., 2016). The effects of habitat changes and diet shifts on the phenotypic traits of a wild ungulate species were demonstrated by a long-term study carried out in southern France (Garel *et al*., 2007). By analysing the consequences of habitat loss on body mass, horn size and horn shape of mouflon (*Ovis gmelini musimon*), the authors reported that changes in quality and availability of food resources were crucial to the decline in phenotypic

quality of mouflon. Our results support this finding, as male ibexes inhabiting shrub- and grass-rich open areas (cluster 2) are characterized by longer annual segments than those inhabiting forest and closure habitats (cluster 1). Surprisingly, the horn growth rates decreased faster with advancing age in males sampled in shrub- and grass-rich open areas than in males sampled in forest and closure habitats. This result suggested that males may face a trade-off limiting horn growth or that once a horn size threshold is achieved, further growth has no effect on male performance. However, the exact causes for this trend are difficult to pinpoint as more detailed information is lacking.

There are some possible explanations, ranging from ontogenetic to environmental, to explain the effects of temporal and spatial variability of forage quality in alpine ungulates. First, seasonal and environmental-driven variations in forage availability/quality may lead to poor maternal cares during prenatal and postnatal stages, which affects offspring mass and survival (Landete-Castillejos *et al*., 2009). Second, because the synchrony of parturition time plays an important role in among-individual variation, too early or too late neonates may mismatch the peak of vegetation productivity and/or climate mildness (Feder *et al*., 2008). This seems to be set a vicious circle as early nutritional deficits can have negative effects on the adult survival and its offspring (Burton & Metcalfe, 2014).

The absence of compensatory horn growth has important implications for the Iberian ibex management because (i) young males presenting a smaller horn growth are not able to recover from a bad start and will become small-horned mature males and, (ii) the species is more prone to suffer strong evolutionary effects of trophy hunting (Festa-Bianchet, 2016). Although this result corroborates previous findings, there are some considerations worth highlighting. The traits measured to evaluate compensatory horn growth in most studies (*e.g*. horn length), including our own, are often the most accessible and seldom the most functional. Few studies explored other horn growth parameters (*e.g*. apical/base circumference, segment volume) to test the occurrence of this mechanism (see Festa-Bianchet *et al*., 2004), which prevents generating conclusive remarks (Sarasa *et al*., 2012). The fighting behaviour of male Iberian ibexes poses a strong pressure on the basal sections of horns, so horn volume is considered an important feature to maintain the integrity of these structures

(Álvarez, 1990). High-quality males with massive horns fight for longer times and are best suitable to withstand heavy blows from other males. This gives an important competitive advantage on female choice and mating partners' defense. Horn volume is therefore an important trait that might be safeguarded. An alternative hypothesis can be proposed to explain the absence of compensatory horn growth. For instance, harsh environmental conditions during early growth affect all individuals of the same cohort simultaneously (Hamel *et al*., 2016). Therefore, allocating a substantial amount of resources to compensate horn growth in adverse environments might not be a good strategy once all the male competitors shared the same environmental constraints and it can entail survival costs. This conservative strategy of resource allocation that tracks environmental variation and resource availability is usually displayed by large herbivores inhabiting seasonal environments (Descamps *et al*., 2016). In this case, the genetic and parental effects can make the difference between small-horned and large-horned mature males. Additionally, recent studies reported a significant reduction of male–male interactions during the mating season (Willisch & Neuhaus, 2010) and showed that young adults of male Alpine ibex participate in the rut through coursing, a low-cost reproductive tactic (Willisch & Neuhaus, 2009). This energetically conservative reproductive behavior, that still needs to be confirmed in the Iberian ibex, makes the recovery of horn size throughout life an optional strategy with unnecessary survival costs.

Our study is correlative which represents an important caveat to our analyses. We do not control for genetic effects, that may represent an evolutionary constraint to compensatory horn growth, or for the nutritional value of vegetation units, which hampers the description of the relationships between differences in habitat characteristics and the possibility of compensatory horn growth. Experimental long-term studies need to be run in order to shed light about cause-effect relationships of compensatory horn growth in ungulates. Because trade-offs in relative allocation depends on environmental conditions and total resource acquisition (Descamps *et al*., 2016), we argue that compensatory horn growth may be adaptive and contingent on region. We also advocate that future approaches beholding a geographically extensive sampling and the incorporation of ecologically, epidemiologically and genetically related variables, as well as the study of others morphological parameters, are

increasingly necessary to understand the long-term consequences of size-selective harvesting and nutritional deficits on horn growth patterns of *Caprinae* populations. Nevertheless, we demonstrated that habitat characteristics are one of the key variables that foster significant differences in the males' horn length. This information is of great interest for hunting associations and wildlife managers as it provides scientific support for design habitat management actions aimed at improving the phenotypic quality of male ibexes and mitigating the impacts of trophy hunting.

CHAPTER 4 Habitat management is key to the sustainability of trophy hunting in Mediterranean ecosystems

* The Mediterranean ecosystem of *Els Ports de Tortosa i Beseit*. Photo: João Carvalho.

Abstract

Size-selective harvesting of wild ungulates can trigger a wide range of ecological and evolutionary consequences. However, it remains unclear if, and if yes how, environmental conditions, including changes in habitat and climate, dilute or strengthen the effects of trophy hunting.

We analyze annual and total horn length measurements of 2,815 male ibexes (*Capra pyrenaica*) that were harvested between 1995 and 2017 in the *Els Ports de Tortosa i Beseit* National Hunting Reserve*,* northeast Spain. We used linear mixed models to determine the magnitude of inter-individual horn growth variability and partial least square path models to evaluate long-term effects of hunting strategy, environmental change and population size on horn growth.

Age-specific, total horn length significantly decreased over the study period (β = -0.085, P = 0.05), and nearly a quarter (23%) of its annual variation is attributed to individual heterogeneities among males. The encroachment of pine forests had a negative effect on annual horn growth (β = -0.092, P < 0.05), possibly through nutritional impoverishment. The harvesting of small-horned males increased horn growth (β = 0.108, P < 0.05), probably because it reduces the competition for resources and prevents breeding of smaller males. Non-significant influences were found for climate (β = -0.022, P = 0.60) and population size (β = -0.037, P = 0.410).

Our study allows to translate an increased knowledge of how habitat change is altering the horn growth of male ibexes into amenable management measures. Our results suggest that habitat interventions, such the thinning of pine forests, can contribute to securing the sustainability of trophy hunting. Even in situations where size-selective harvesting isn't causing a detectable phenotypic response, management actions leading to the expansion of preferred habitats, such as grass-rich open areas, can have a positive effect on ungulate fitness. The forest encroachment of open meadows and heterogeneous grasslands is pervasive throughout Mediterranean ecosystems. Therefore, our findings can be extended to the landscape level, which will have the potential to mitigate the side effects of habitat deterioration on the phenotypic traits of wild ibexes.

Keywords *Capra pyrenaica*, forest encroachment, horn size, hunting management, monitoring, mountain ungulates, size-selective harvesting, Spain.

4.1. Introduction

Trophy hunting of wild ungulates can be an important source of income and may even generate significant revenues for conservation (Johnson, 1997; Leader-Williams, 2009), particularly in those areas where ecotourism is economically or politically not viable (Lindsey *et al*., 2007). For instance, Lindsey (2008) estimated that trophy hunting in sub-Saharan Africa generated profits of approximately US$201 million per year. Although intense trophy hunting can trigger phenotypic and evolutionary trait changes in wild bovids (Coltman *et al*., 2003; Pigeon *et al*., 2016), it remains largely unexplored if, and if yes how, individual performance, population structure and composition, as well as a multitude of environmental factors, including habitat changes, weaken, counterbalance or strengthen these effects (Heffelfinger, 2018a; but see Kardos *et al*., 2018). Trophy hunting may hinder population productivity, recovery and yield. Therefore, understanding the effect of biotic and abiotic variables on phenotypic-trait changes is essential to manage wild bovid populations more effectively, guaranteeing the long-term sustainability of hunting systems.

The management of wild bovid populations in a world facing ever-faster environmental changes has been a matter of intense debate (Boyce & Krausman, 2018). First, it is difficult to disentangle if trait changes are due to genetic effects or phenotypic plasticity, even considering that plastic alternations occur faster than evolutionary changes (Merilä & Hendry, 2014). Second, the absence of fine-scale variables amenable to management in the analysis of trait changes could lead to noticeable caveats in determining the relative contribution of different factors for the phenotype of wild bovid populations. Although the influence of habitat loss, resource availability and/or population density on phenotypic trait-changes could be diluted at broad geographic areas, their inclusion is crucial when studies are conducted at narrow spatial scales (Monteith *et al*., 2013). Third, the variability between populations regarding those factors that influence the size and shape of phenotypic traits is overwhelming. Analyzing long-term datasets compiled from wild bovid populations subjected to trophy hunting and environmental changes is therefore increasingly relevant to design fine-scale management strategies. However, there is only a handful of suitable datasets available worldwide that

are well-replicated and long enough to assess the long-term consequences of size-selective harvesting and environmental changes on the phenotypic changes at individual and population levels (Festa-Bianchet *et al*., 2017). In fact, comprehensive hunting inventories are geographically biased and much of what is known on this subject remains confined to some regions and habitats. We still lack studies of how human practices and environmental factors influence the phenotypic traits of trophy hunted ungulates. This is particularly the case for Mediterranean ecosystems (Pérez *et al*., 2011a), where climate, phenology and management regimes differ from those recorded in North America and northern Europe.

In Spain, there is a long tradition of wild ungulate hunting (Pérez *et al*., 2002; Acevedo *et al*., 2009; Fandos *et al*., 2010b), with the iconic Iberian ibex (*Capra pyrenaica*) being the most desirable target among all game species. There are no reliable estimates of revenues produced by the size-selective hunting of male ibexes. The starting price auction (*C. p. victoriae* – aprox. €5,650 and *C. p. hispanica* – approx. €3,120), however, is a good indicator of the economic value of the species (Sarasa, 2013). Annual revenues can reach €322,000 to support rural economies (Junta de Castilla y León archives). The trophy hunting of male ibexes takes place nearly all over the species range and occurs during the mating (December – January) and spring season (March – May). Since the early 70´s, in particular, the Iberian ibex have been explored by a network of national and regional game reserves in northeastern (*Els Ports de Tortosa i Beseit*), western (*Sierra de Gredos* and *Batuecas*) and southern (*Sierra de Cazorla Segura y las Villas*, *Tejeda Almijara* and *Sierra de Ronda*) Spain. The hunting permits are obtained directly from autonomous governments, county councils or private land owners and are generally attributed to hunters from all over the world. By means of trading long-term sustainability for short-term economic return, some game keepers may have focused on the harvesting of large-horned males (Pérez *et al*., 2011a). The Mediterranean ungulate populations, including the Iberian ibex, are also confronted with several environmental constrains that may influence the genetic effects of hunting selection. The western Mediterranean basin experiences an increasing aridity since the 1970s (Kelley *et al*., 2012). Rising temperatures together with decreasing precipitation and agricultural land abandonment

impact the landscape configuration by promoting the encroachment of grasslands by drought resistant woody shrubs (Peñuelas *et al*., 2017). The loss of grass-rich open areas caused a decrease in the resource quantity and quality for grazers and mixed-feeders, such as ibex (Martínez, 1994, 2000). In order to shed light on the multitude of genetic and nongenetic factors that cause phenotypic trait changes in wild ungulates, several studies have recently reported the importance of long-term hunting inventories (Büntgen *et al*., 2014; Pigeon *et al*., 2016; Douhard *et al*., 2017; Büntgen *et al*., 2018). Although such studies provide guidance for management and open new research avenues, some of them focused on particular genetic or environmental aspects and thus failed to disentangle the direct and indirect pathways by which environmental conditions, density-dependency and hunting strategy affect specific traits.

Here, we analyze the horn length of 2,815 male ibexes that were harvested in northeastern Spain between 1995 and 2017. This unique dataset allows us to evaluate the long-term phenotypic consequences of local weather conditions (Hypothesis 1), habitat structure (Hypothesis 2), density-dependency (Hypothesis 3) and hunting strategy (Hypothesis 4) on horn length of male ibexes (**Table 5**). Since the different factors are not operating exclusively, we use a path modelling approach to account for direct and indirect causal effects.

Table 5. Hypothesis, rationale and predictions on the variables that potentially drive phenotypic variations of horn size in Iberian ibex.

Hypothesis		Rationale	Prediction	Variables	Code
Local weather conditions (H1)	**Synergistic effects**	Local weather patterns strongly determine the availability of forage. Precipitation, ambient temperature and snow persistence influence the plants phenology and, therefore, the reproductive performance, the demography and the phenotype development of wild ungulates (Buntgen *et al*., 2014; Plard *et al*., 2014).	The climate warming has amplified the Mediterranean drying since the 1970s (Buntgen *et al*., 2017). We postulated that the rising of temperatures and dryness have a negative impact on horn growth of bovid populations inhabiting a typical Mediterranean ecosystem.	Köppen aridity index (Green-up)	KAridIGU
				Köppen aridity index (Senescence)	KAridISN
Habitat structure (H2)		The favorability of natural habitats mainly relates with the quantity and quality of food resources that they can provide. Habitat loss due to natural succession or socioeconomic changes can boost alternative evolutionary trajectories. In species characterized by a considerable phenotypic plasticity, habitat changes potentially affect the expression or size of certain traits (Garel *et al*., 2007).	Forest encroachment and the ongoing loss of grass-rich open areas have been observed over the last decades in PTB. We expected a general decrease in horn size as a response to habitat deterioration.	Coniferous forests (%)	ConF
				Shrubs (%)	Shrbs
				Natural pastures (%)	NatP
Density-dependence factors (H3)		The competition for food resources occurs whenever population density goes beyond the carrying capacity of an ecosystem. High densities impact the plant productivity, the nutritional value of vegetation and may have far-reaching consequences on the dynamics, performance and phenotype of wild ungulate populations (Pérez *et al*., 2011a).	After a population management process at the beginning of 1990´s, the Iberian ibex population of PTB is now considered stable. We therefore hypothesized that the role of population size on the potential variations of horn size is null or residual.	Population size (N)	PSize
Hunting strategy (H4)		Unrestrictive and poorly managed trophy and selective hunting has been considered a dominant force for the rapid evolutionary or phenotypic change in wild ungulates (Pigeon *et al*., 2016). Trophy hunting, in particular, caused a decrease in the mean breeding values for weight and horn size	The offtake of trophy males has decreased in the PTB, which may reduce the chances of a human-induced phenotypic response. Moreover, the harvesting of small-horned young males could dilute the selective effects of trophy	Trophy males	TMale
				Selective individuals	SInd

	(Coltman *et al*., 2003).	hunting (Mysterud & Bischof, 2010). Our expectations are that hunting pressure plays a minor role on potential phenotypic changes.	

4.2. Material and methods

4.2.1. Study area and hunting system

The Iberian ibex population of the *Els Ports de Tortosa i Beseit* National Hunting Reserve (hereafter PTB), northeastern Spain, is an ideal case to test our four hypothesis because (i) the study area is characterized by a controlled harvesting system where the length of each annual horn growth segment was recorded by a team of game wardens, that follow a strict measurement protocol, (ii) differences in the horn dimensions of male ibexes are obvious for managers and hunters, which make this species particularly susceptible to the side-effects of trophy hunting, (iii) horn measures are available not only for trophy males but also for small-horned yearlings and adults, and iv) habitat closure and the loss of nature pastures are widespread.

Covering an area of 28,587 hectares (**Figure 15**), the PTB was created in 1966 and is characterized by a rugged and highly heterogeneous landscape with elevation ranging from 300 to 1,442 m.a.s.l. The average annual temperature is around 14 ºC and the mean annual total precipitation is 700 mm. PTB encompasses a range of Mediterranean-type habitats of *Quercus ilex* and *Pinus halepensis* forests, interspersed by pastures and crops. The evergreen sclerophyll shrubland predominates in the eastern PTB. Over the last decades, this area has experienced severe socioeconomic changes that led to the abandonment of livestock and agricultural practices, with the conversion of natural pastures and open scrublands into dense pine woods, *i.e*. forest encroachment (Vargas & Vila, 2005). Yet, management measures oriented to improve habitat quality of ibexes have never been implemented in PTB.

Currently, the Iberian ibex hunting in PTB is managed by a technical management plan based on standardized surveys and population trends. Hunting permits can be classified as trophy, male selective or female selective. Selective hunting aims to limit population density and to perform health surveillance and management. Hunting quota are divided into an entry quota, which is independent of the hunting outcome, and a supplementary quota that depends on the trophy quality. An additional tax is reserved for those cases

where an animal is shot but cannot be recuperated. The hunters have two days to hunt a trophy male and just one day to hunt a selective individual, either male or female. The hunter is permanently accompanied by a game warden responsible for any hunt operation and decision. The game warden decides which animals can be harvested at a given time. The Commission of Homologation of Hunting Trophies defines a trophy ibex by its horn length, basal horn perimeter and age. The trophies are classified into three categories: bronze medal (205.00 to 214.99 points), silver medal (215.00 to 224.99 points) and gold medal (above 225.00 points). For the sake of effective management, PTB is divided into smaller patches called spots (n = 50), that present a significant variability in terms of habitat characteristics, topography and population size (**Figure 15a, b, c**). As adult Iberian ibexes in PTB are sedentary, we considered that the individuals were harvested in the spot where they spend most of their lifetime (Escos & Alados, 1992). Such information is important when assessing spatial variations in horn growth and to describing the human-induced and environment pressures experienced by each individual during the period of interest.

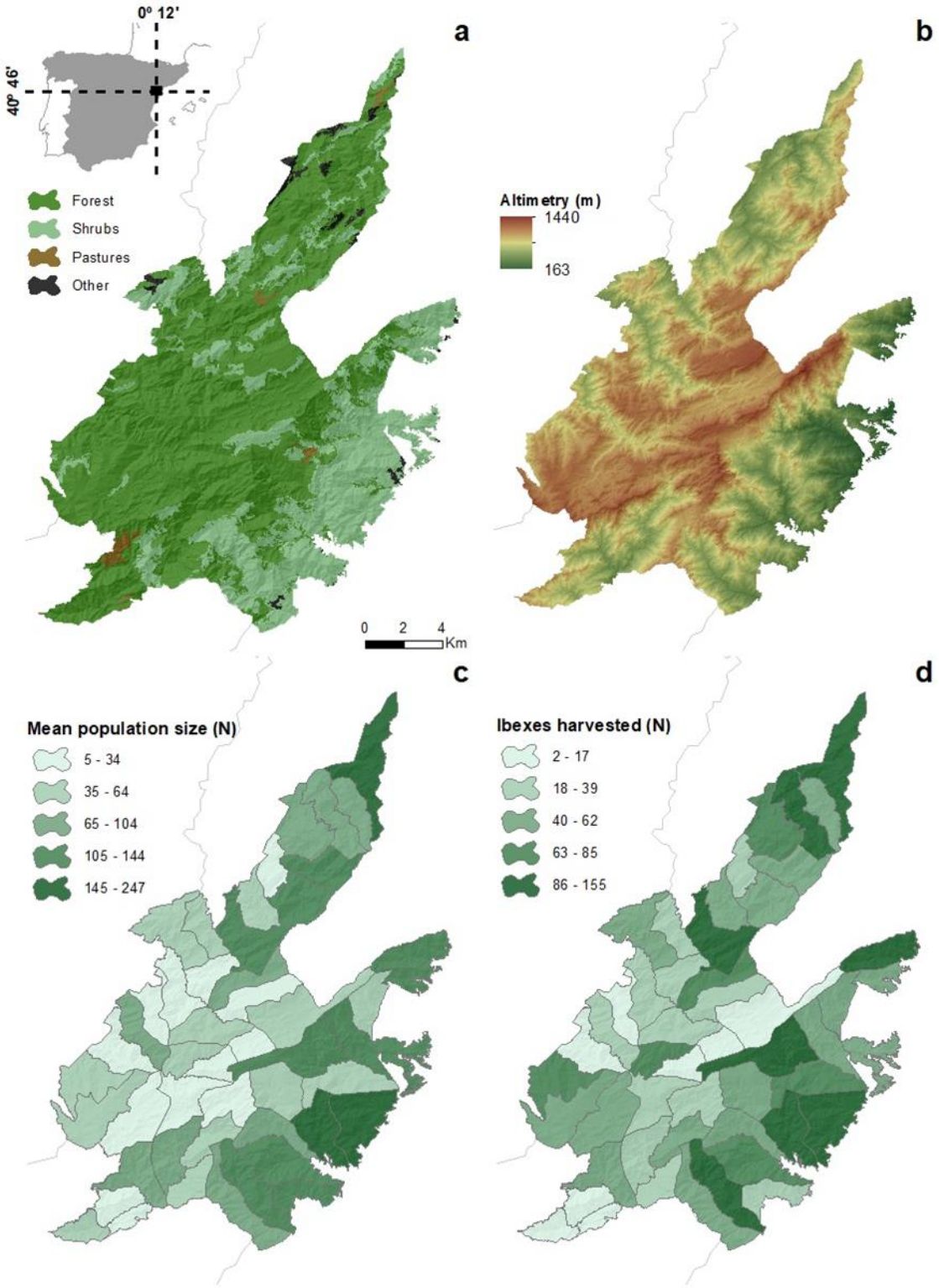

Figure 15. Location of the *Els Ports de Tortosa i Beseit* National Game Reserve, northeastern Spain, with indication of main land uses **(a)**, altimetry **(b)**, mean population size per spot **(c)** and total number of males harvested per spot over the study period **(d)**.

4.2.2. Horn growth measurements

The samples considered in this study are an update of the dataset presented by Carvalho *et al*. (2017). The male ibexes were legally hunted by registered hunters over 22 years (1995 – 2017). This time span includes the 1979 - 2012 cohorts. During the sampling period, measures and samples were retrieved from 2,815 male ibexes aged between 1 and 17 years, and evenly distributed over the study area (**Figure 15d**). We measured a total of 31,813 annual horn growth segments. Unfortunately, horn growth information is not available for the three consecutive years 2001, 2002 and 2003. The number of male ibexes harvested per year varied between 65 and 203 in 2013 and 2007, respectively (**Figure 16a**). For each male, the annual horn growth measurements were taken at the outer lateral side using a millimeter-precise nylon tape. Measurement uncertainty between the individual observers is negligible as a strict standardized protocol was considered. The outermost annual growth segment was excluded from our analyses due to abrasion (Álvarez, 1990; Büntgen *et al*., 2014, 2018) and maternal effects (Giacometti *et al*., 2002). The average age of most of the ibexes resulted in 10-15 growth segments per horn (**Figure 16b**). In this study, we only considered the first 2-8 annual horn segments (L2-L8) to reduce potential biases in the interpretation as a sharp decrease in annual horn growth length occurs after the age of eight (Carvalho *et al*., 2017). Moreover, one-year old males (n = 49) and males of unknown provenance (n = 74) were excluded.

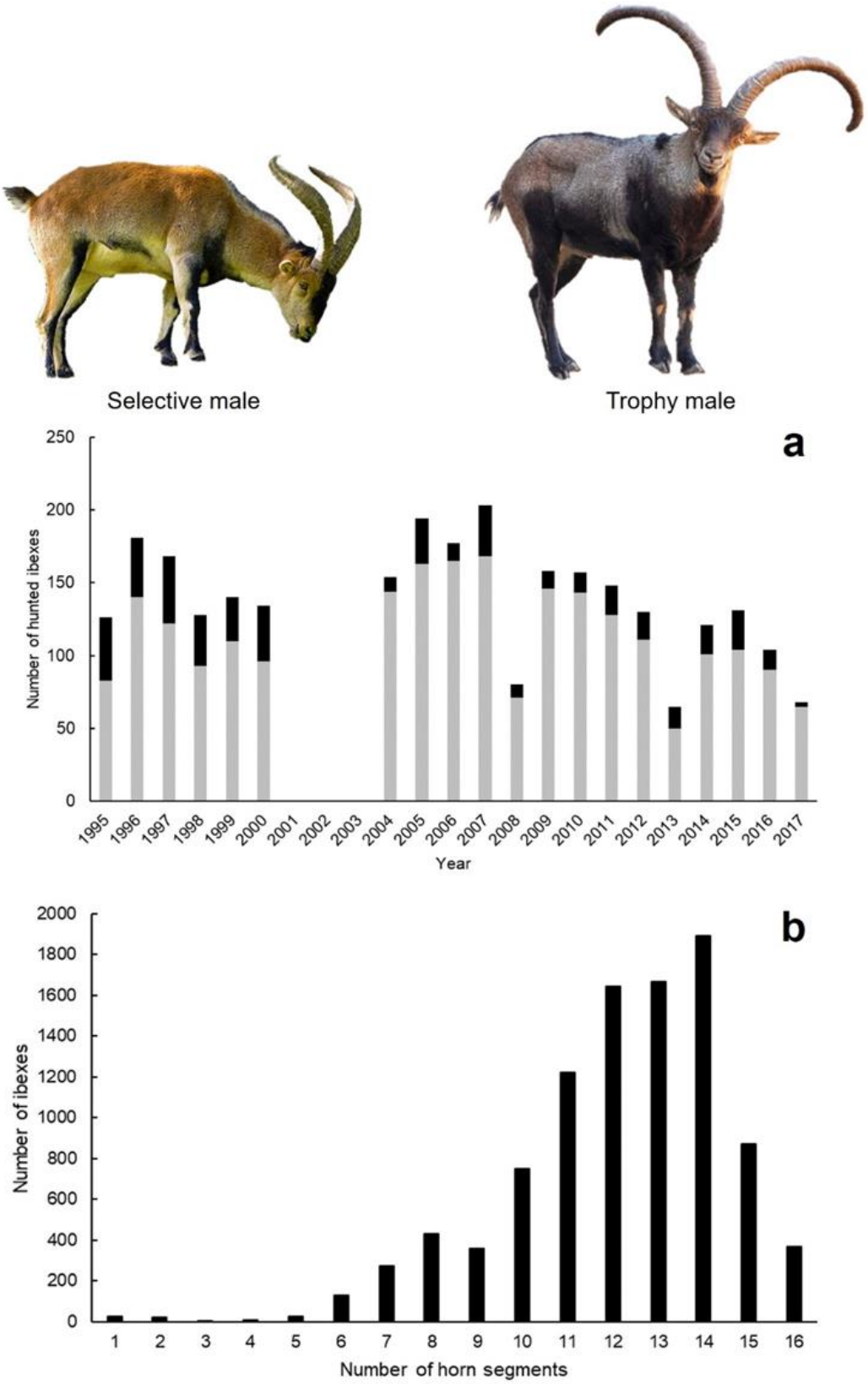

Figure 16. Number of selective (light grey) and trophy (black) Iberian ibex males harvested *per* year in the *Els Ports de Tortosa i Beseit* National Game Reserve, northeastern Spain **(a)** and distribution of 31,813 annual horn growth segments from 2,815 male ibexes **(b)**. Photo: Casals & Jurado, Cròniques Naturalistes.

4.2.3. Environmental factors

Monthly resolved temperature and precipitation data were obtained from the Global Climate Monitor (http://www.globalclimatemonitor.org/). The mean annual temperature and total precipitation were used to calculate regional drought conditions via the Köppen Aridity Index (KAI; Köppen, 1923; Quan *et al*., 2013). We calculated the KAI for two periods of particular relevance for horn growth: the spring-summer or the green-up period (April-September) and the winter or the senescence period (November-March) as horn growth patterns are age- and season-dependent, *i.e*. spring-summer conditions are those experienced by males during the growth stage, while winter conditions determine the vegetation productivity of the following seasons.

The land cover map of Catalonia (LCMC) was gathered from the Centre de *Recerca Ecològica i Aplicacions Forestals* (CREAF, http://www.creaf.uab.es/mcsc/usa/index.htm). LCMC corresponds to a high-resolution database that guarantees the partial temporal coverage of the study period. Currently, LCMC has four editions (1956, 1993, 2005 and 2009). We divided our study area in three main categories: forest stands, which are mainly composed by coniferous forests of *Pinus halepensis*, *Pinus nigra* and *Pinus sylvestris*, shrubs (*e.g*. sclerophyllous vegetation and transitional woodland shrub) and natural pastures (*e.g*. natural grassland and sparsely vegetated areas). Forest stands are an indicator of habitat deterioration, representing less suitable areas in terms of resources availability and quality (Scooter, 1980). Shrubs and pastures provide important food resources and are habitats of high-visibility, which increases the chances of identify potential threats. The percentage of each category was calculated for each spot. As nutritional intake is pivotal to horn growth (Heffelfinger, 2018a), we determined the diet quality of 94 male ibexes by means of faecal nitrogen, a proxy of diet quality in mammalian herbivores (Leslie *et al*., 2008). Our main is to establish, not only a correlative association, but a plausible cause-effect relationship between changes in habitat structure and potential changes in horn size. We advocate that coniferous forests are nutritional poor, which will be reflected in lower horn sizes. A detailed description of the methodology can be found in the Appendix A.

4.2.4. Population size estimates

The Iberian ibex population surveys in PTB were carried out between 1996 and 2017. The censuses were conducted at the end of winter by five teams of two observers. Precise data on population size and population structure per spot were collected using two complementary methodologies: line transects and vantage points. At the end of each daily session, the observers cross-checked the information to eliminate repeated observations. Population size, estimated as the total number of males, females and calves, was used to account for the density-dependent effects on horn growth. Taking advantage of reliable estimates of population size, we calculated the hunting pressure as the proportion of individuals that were removed from the population. We considered the proportion of harvested males that were graded as trophies and the proportion of individuals, males and females, which were harvested under the selective hunting modality.

4.2.5. Statistical analysis

The non-parametric Mann-Kendall test was applied to detect potential temporal trends in the various predictor variables. We visually investigated the autocorrelation and the partial autocorrelation of each time series. If a particular time series was autocorrelated, the Mann-Kendall test was applied via the block-bootstrap method. The Mann-Kendall test was carried out using the "*Kendall*" version 2.2 (McLeod, 2011) and "*boot*" version 1.3-20 (Ripley, 2017) packages in *R*.

Horn growth analysis was performed in three phases. Firstly, we updated the results reported by Carvalho *et al*. (2017), by exploring the total horn length and the length of each annual segment as function of age. Secondly, we fitted a set of linear mixed models (LMMs) to explore individual heterogeneities in male horn growth. The animal ID and the spot were set as random intercept factors to account for repeated measurements (Zuur *et al*., 2009). As animal ID and spot are hierarchically structured, that is each animal ID is assigned to the respective provenance, we implemented the LMMs with nested random effects. Model

selection was based on the Akaike Information Criterion (AIC; Akaike, 1974; Burnham & Anderson, 2002). The LMM analyses were carried out using the "*lme4*" package version 1.1-17 (Bates *et al*., 2018) and the "*MuMIn*" package version 1.40.4 (Barton, 2015) was used to calculate the marginal and conditional R^2. We applied the likelihood ratio test (LRT) to assess the significance of the random factors for horn growth differences and we estimated repeatability to quantify the individual and spatial contribution to horn growth variability. The R package "*rptR*" version 0.9.21 was used to perform the likelihood ratio test and to estimate repeatability (Stoffel *et al*., 2018). Finally, as environmental conditions, density-dependence factors and hunting strategy can affect the horn growth through several direct and indirect pathways, we used partial least square path models (PLS-PM, Sanchez, 2013) to simultaneously examine the importance of these pathways on the length of the horn segments. PLS-PM is comprised by two sub-models: the inner or structural model and the outer or measurement model (Tenenhaus *et al*., 2005). The inner model expresses the relationships between the latent variables or constructs (*e.g*. a set of weather indicators defining an abstract concept such as "Weather conditions"). The outer model relates the manifest variables or indicators (*i.e*. variables directly measured in the field) to their own latent variables. Our inner model is composed by five latent variables accounting for the response variable (the length of the horn segments), local weather conditions, habitat characteristics, population size and hunting strategy. As the latent variables are formed by its indicators, we defined that the measurement of the latent variables is in reflective mode. The model was fit using the "*plspm*" package version 0.4.9 in *R* (Sanchez *et al*., 2015). All statistical analyses were performed using the statistical software *R* 3.3.0 (R Development Core Team, 2017).

4.3. Results

4.3.1. Temporal trends of environmental variables

Non-significant temporal trends were found for the KAI (KAridIGU: τ = 0.036, P = 0.753; KAridISN: τ = -0.093, P = 0.410). With respect to land cover

and habitat characteristics, we observed a pervasive conversion of natural pastures and open scrublands into dense pinewoods. In 1993, pinewoods represented approximately 50% of the study area. Between 1993 and 2009, while the Mediterranean scrubs and natural grasslands decreased by 14%, pinewoods increased by 13%. Forest encroachment was not limited in space and was reported for the whole PTB. The rate to which pine encroachment occurred was, however, contingent on the area. In the southeast of PTB, we recorded an increase of pinewoods in the rough order of magnitude of around 12-30%. Although still dominated by Mediterranean shrubs, this area has been progressively occupied by pine trees. Shifts from scrubland and grassland to pine forests has been less pronounced along the western border of the study area. However, this area was already dominated by dense forests of *Pinus halepensis* in the past, which explains this result.

4.3.2. Population size and hunting pressure

The number of ibexes decreased significantly (τ = -0.743, P < 0.001) over the study period. The population census suggested a decrease in abundance of approximately 25% between 1997 and 2017. We also recorded a significant reduction in the number of ibexes harvested, both trophy males and selective individuals. The number of trophy ibexes declined sharply between 1995 and 2008, and then remained constant afterwards (τ = -0.533, P < 0.001). The number of selective ibexes, however, revealed a linear decrease over the last 22 years (τ = -0.692, P < 0.001).

4.3.3. Horn growth patterns

Our analysis corroborates the horn growth patterns previously reported. Male's age drives total horn length (β = 3.48, SE = 0.06, t = 53.81, P < 0.0001, R^2 = 0.54, **Figure 17a**) and the annual segment length decreases after the age of eight (β = -0.20, SE = 0.006, t = -32.47, P < 0.0001, **Figure 17b**). The LRT identified the male identity as highly significant in the mixed model of segment length (LRT = 1160, P < 0.001). We found that individual differences account for

23% of variation in annual horn growth. We recorded a fell in repeatability estimates to around 21% when the spot was included as a random effect, which suggests that a proportion of among-individual differences in horn length were caused by environmental conditions and spatial heterogeneities.

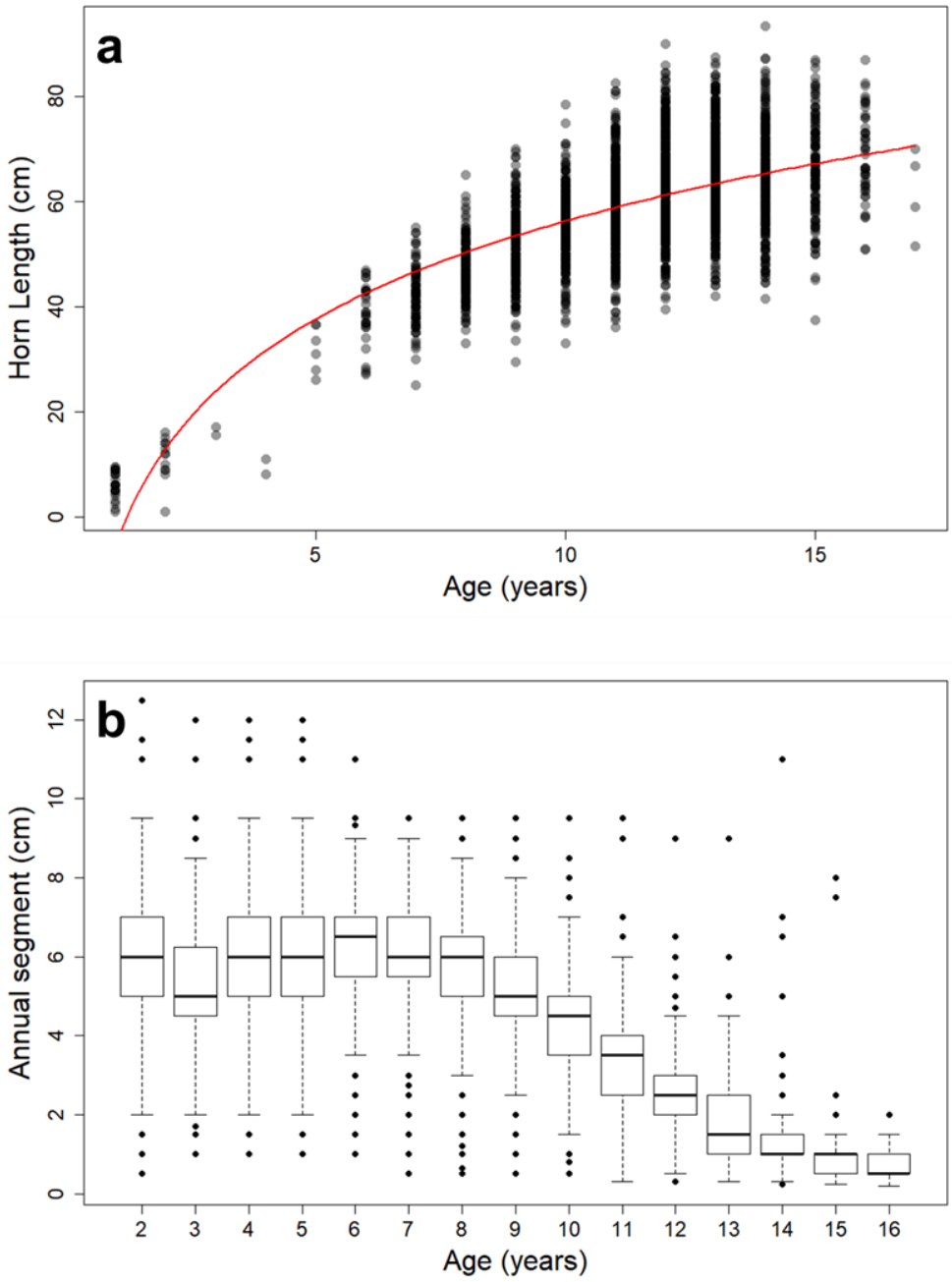

Figure 17. Horn growth patterns of 2,815 male ibexes from the *Els Ports de Tortosa i Beseit* National Game Reserve, northeastern Spain. Plots represent the relationship between total horn length (cm) and age at harvest (years) **(a)**, and the relationship between annual segment length (cm) and male's age (years) **(b).**

4.3.4. Environmental and hunting effects on annual horn growth

Our PLS-PM indicate a consistent downward trend of horn size over the last decades (β = -0.085, SE = 0.044, t = -1.94, P = 0.05). The results provide statistical support for the effects of habitat structure (Hypothesis 2) and hunting strategy (Hypothesis 4) on the length of annual segments. However, we found no evidences for a statistically significant effect of local weather conditions (Hypothesis 1) and population size (Hypothesis 3) (**Figure 18**). As regards environmental conditions, we did not detect any statistical evidence that aridity influenced annual horn growth (Hypothesis 1: β = -0.022, SE = 0.042, t = -0.530, P = 0.60), however, PLS-PM coefficients indicate that forest encroachment and the consequent loss of shrubs and grass-rich open areas have a negative and significant effect on annual horn growth (Hypothesis 2: β = -0.092, SE = 0.046, t = -2.000, P < 0.05). Population size does not seem to influence horn growth, which corroborates our prediction (Hypothesis 3: β = -0.037, SE = 0.045, t = -0.824, P = 0.41). Finally, our results suggest that the hunting strategy in PTB, which consists in reducing the removal of trophy males and increasing the offtake of undesirable phenotypes, have a positive and significant effect on annual segment length (Hypothesis 4: β = 0.108, SE = 0.041, t = 2.610, P < 0.05). Even though we tested for indirect pathways by which environmental conditions, density-dependency and hunting strategy affect horn growth, we did not record any statistically significant result (**Figure 18**). Overall, the direct and indirect effects of environmental conditions, population size and hunting strategy explained 18% (R^2 = 18%) of annual horn growth. The decomposition of R^2 shows that hunting strategy and habitat structure are the most important variables accounting to 13.76% and 9.33% of the R^2, respectively. The contribution of local weather conditions and population size to R^2 is minimal, 0,36% and 1,22%, respectively.

The cause-effect relationship between habitat structure and horn size was supported by the results of diet analysis (Appendix A). Particularly in the spring, the faecal nitrogen content is positively and significantly associated with the extension of natural pastures (β = 0.081, SE = 0.035, t = 2.301, P = <0.05, **Table S1**, **Figure S4**). The visual inspection of conditional plots is also

indicative of the negative relationship between the diet quality and the extension of coniferous forests.

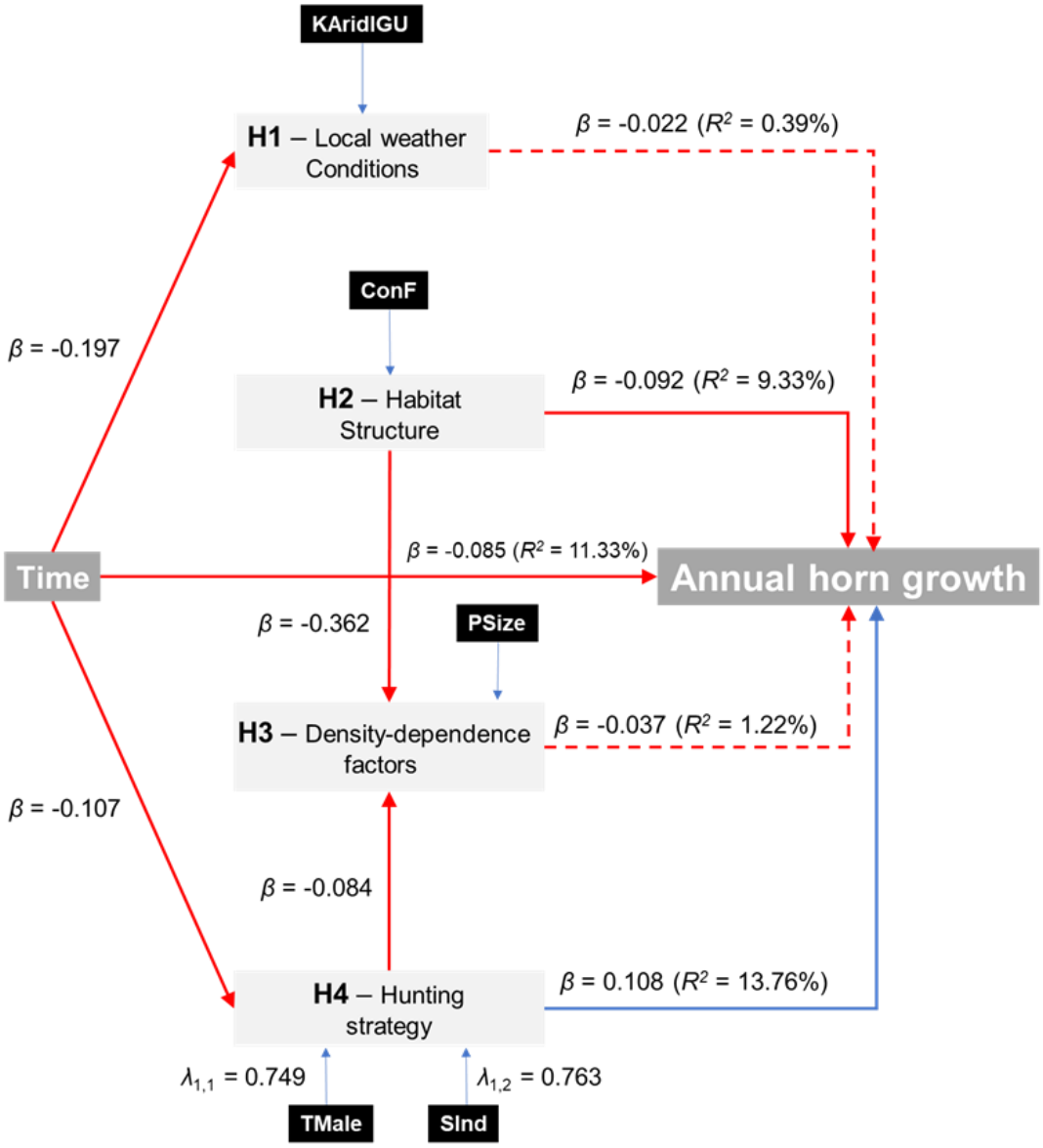

Figure 18. Path model diagram linking time, local weather conditions, habitat structure, density-dependency factors and hunting strategy to annual horn growth in male ibexes harvested between 1995 and 2017 at *Els Ports de Tortosa i Beseit* National Game Reserve, northeastern Spain. Blue and red arrows represent positive and negative relationships between latent variables (light-grey rectangles), respectively. Solid arrows represent significant relationships whereas dashed arrows represent non-significant relationships between variables. The parameter *β* represents the path coefficient between latent variables. Note: KAridIGU - Köppen aridity index (Green-up); ConF - Coniferous forests (%); PSize - Population size (N); TMale - Trophy males (N); Sind - Selective individuals (N).

4.4. Discussion

Our understanding about the causes of phenotypic trait changes is limited because we must consider that wild populations are affected by different, overlapping environmental factors that may or may not act simultaneously to the influences of hunting selection. Our results emphasize the importance of habitat characteristics on the annual horn growth of male ibexes and despite the selection pressure caused by trophy harvest, we found no evidences for a decrease in horn growth motivated by this activity.

Horn growth differed markedly among males of PTB. This is in line with previous studies on Iberian ibex relatives (Bergeron *et al*., 2008; Douhard *et al*., 2017). For instance, individual heterogeneity accounted for circa a quarter of the variability in horn length of Alpine ibex *Capra ibex* (Bergeron *et al*., 2008) and for 17% of the variability in horn length of bighorn sheep *Ovis canadensis* (Douhard *et al*., 2017). The absence of compensatory horn growth in the members of tribe Caprini exacerbate the individual differences among mature males as individuals cannot compensate the growth depression after a period of nutritional deficit (Festa-Bianchet *et al*., 2004; Töigo *et al*., 2013; Carvalho *et al*., 2017). A distinctive feature of our study shows that individual variability in horns' growth is also partially bolstered by the environmental heterogeneities of the study area. Habitat dichotomy in particular seems to contribute for persistent differences in horn size among males, which corroborates a previous study where it was reported that male ibexes inhabiting shrub-dominated areas present longer annual segments than males inhabiting forest patches (Carvalho *et al*., 2017).

We further demonstrate that the downward trend of horn size over the last decades is presumably related to habitat deterioration, here represented by the pine forest encroachment of shrubs and natural grasslands. The loss of grass-rich open areas and the reduction of high-quality food resources have adverse implications in the phenotypic expression of wild bovids (Heffelfinger, 2018a). Surprisingly, little attention has been devoted to the effects of habitat deterioration on horn growth, perhaps because fine-scale land use data that span a long-time frame is lacking. This means that some potential effects of habitat and nutritional changes on trait variations have been missed. The impact

of forage availability and quality on horn development ranges from ontogenetic to direct environmental effects. The lack of food resources may jeopardize maternal cares and therefore the growth and development of the yearlings (Therrien *et al*., 2008). Poor maternal cares and/or the asynchrony between the parturition time and the peak of vegetation productivity can have long-lasting consequences on horn growth because, as reported before, the species of tribe Caprini are not able to compensate from a bad start (Feder *et al*., 2008). The importance of resources availability for horn growth remains high throughout the animals' life, however, it is during the early years of life that resources take a particular significance (Monteith *et al*., 2018). An interesting study on mountain goats (*Oreamnos americanus*) showed that spring forage quality correlates positively with the horn length of yearlings (Gendreau *et al*., 2005). In southern France, it was demonstrated that habitat closure explains part of body mass variations of mouflon lambs (*Ovis gmelini musimon*, Garel *et al*., 2007). The same authors suggest that horn development is less prone to be affected by changes in habitat characteristics, however, both horn size and body mass are energetically demanding for male bovids (Rands *et al*., 2011), meaning that available resources must be balanced between opposing expenditures. The occurrence of tradeoffs in resources allocation is especially likely when the individuals face unfavorable environmental conditions (Festa-Bianchet *et al*., 2004). This evidence can constrain horn growth because the maintenance of individual body mass takes preference in relation to the development of sexual secondary characters. For instance, a long-term study carried out in the Ram Mountain suggested that, in poor years, bighorn males reduce their investment in horn growth and increase the relative allocation of resources to summer mass gain, probably trading-off long-term reproductive success for short-term survival (Douhard *et al*., 2017).

We found no evidences of hunting-induced phenotypic changes. Although this result corroborates our expectations, it should be interpreted with caution. First, our data regarding the number of harvested ibexes is limited in time and the effects of selective harvesting on phenotypic traits can take several decades to be recorded (Coulson *et al*., 2018). Second, our data merely represents a proxy of hunting pressure and no genetic information (*e.g*. selection differential, heritability, pedigree) is available for our population (Kardos *et al*., 2018). Even

though we did not estimate the potential phenotypic variance related to genetic differences, there are some aspects that can weaken the phenotypic and evolutionary responses to trophy hunting. The hunting strategy of our study area comprise the selective harvesting of small-horned males, which has been suggested to counteract the selective effects of trophy hunting because it reduces the competition for space and food resources and prevents the breeding of smaller males (Mysterud & Bischof, 2010). Even though we did not detect any effect of population size on horn growth, the positive influence of removing small-horned males on this trait suggested that some effects related with population density may be missed. Moreover, the gene flow caused by the dispersal of males from areas freed from hunting selection or subjected to lesser intense selection would be important to minimize the evolutionary effects of selection (Lenormand, 2002). The lack of evolutionary responses through selective trophy hunting was also reported from the eastern Swiss Canton Grisons, where the harvesting of Alpine ibexes follows a strict regulation (Büntgen *et al*., 2018).

We do not detect any effect of local weather conditions on horn growth patterns, however, previous studies reported a significant correlation between climate and the horn growth of wild ungulates (Cantabrian chamois *Rupicapra pyrenaica parva*, Pérez-Barbería *et al*., 1996; Dall's sheep *Ovis dalli dalli*, Hik & Carey, 2000 and Loehr *et al*., 2010; bighorn sheep, Hedrick, 2011 and Douhard *et al*., 2017; Iberian ibex, Pérez *et al*., 2011a; Alpine ibex *Capra ibex ibex*, Giacometti *et al*., 2002; von Hardenberg *et al*. 2004; Büntgen *et al*., 2014). The climate trend towards overall dryer conditions might decrease the extent of heterogeneous grasslands and consequently increase the competition for food resources. As recent scenarios foresee the ongoing loss, fragmentation and degradation of Mediterranean grassland areas over the upcoming years (Mairota *et al*., 2013), we stress the need of continuing monitoring protocols to disentangle the effects of climate conditions on phenotypic traits of wild populations.

4.5. Conclusions and implications

In Spain, the size-selective harvesting of male ibexes extends nearly all over the species range, however, the importance of habitat characteristics and food availability on horn growth patterns have been widely overlooked by national and regional hunting reserves (Fandos *et al*., 2010b). Despite some constraints (*e.g*. limited timeframe of the dataset and absence of genetic data), our results provide support to prioritize management actions related with habitat structure and hunting strategy. Pine forest encroachment had a significant negative impact on horn growth, probably due to dietary shifts, nutritional deficits and an increasing competition for resources. Even though habitat effects were demonstrated at a limited scale, our findings can be extended to the landscape scale as the forest encroachment at the expense of shrubs and grass-rich open areas occurred at unprecedented rate throughout Mediterranean ecosystems (Peñuelas *et al*., 2017).

The monitoring of habitat changes must be on the game managers agenda. This is particularly important because the consequences of nutritional condition are easily recognized by regular monitoring and could be adjusted by appropriate management measures (Monteith *et al*., 2018), such as the creation of open areas of high herbaceous richness and the improvement of forest edges. Prescribed burning has long been seen as a common practice in Mediterranean towards high productivity and palatability of forage, however, poses clear risks and should be used only in specific locations. Logging and thinning of forest patches are expected to improve shrub and herbaceous vegetation, while conserving the structure-related habitat features essential for protection and shelter. Future habitat management plans should recognize that each vegetation type has a particular potential for supporting wild ungulates and should consider expected scenarios of drought in order to improve the resilience of Mediterranean shrublands and grasslands to climate (Granados *et al*., 2016). Whenever habitat deterioration is irreversible and/or poses expensive long-term actions, we suggest the application of measures aim to manipulate the animal numbers. This will adjust the population size to habitat carrying capacity. An important take home message is that horn growth in Caprinae continues throughout the animal's life, thus game managers should understand

that a single year of nutritional deficits could limit the phenotypic potential of an entire cohort.

We did not find any negative relation between trophy hunting and horn growth patterns, but we are aware of a possible phenotypic and/or evolutionary response to trophy hunting. We suggest the creation of harvest refuges and the protection of some younger males that exhibit a great early horn growth to allow them to peak reproductively (Kardos *et al*., 2018). This will guarantee the short-term sustainability of the hunting practice, while the long-term planning based on habitat improvements is carried on.

Finally, we argue that a serious long-term commitment of game reserves is the most welcome step towards to (i) detect age-related changes in life-history traits, (ii) deepen our understanding on the effects of human-induced and/or environmental changes on growth variations, (iii) determine if breeding success is determined by specific traits (*e.g*. determine to what extent males of lower phenotypic quality are able to mate) and (iv) estimate the genetic variance of specific traits and the effects of exogenous sources of stress on the phenotypic expression. We therefore encourage all managers and game wardens to record, at least, the measure of each horn growth segment as it reflects short-term environmental fluctuations.

CHAPTER 5 Sarcoptic mange breaks up bottom-up regulation of body condition in a large herbivore population

* Mildly infested ibex presenting extensive alopecia on the face, abdomen, elbow and knees. Photo: José Enrique Granados.

Abstract

Both parasitic load and resource availability can impact individual fitness, yet little is known about the interplay between these parameters in shaping body condition, a key determinant of fitness in wild mammals inhabiting seasonal environments.

Using partial least square regressions (PLSR), we explored how temporal variation in climatic conditions, vegetation dynamics and sarcoptic mange (*Sarcoptes scabiei*) severity impacted body condition of 473 Iberian ibexes (*Capra pyrenaica*) harvested between 1995 and 2008 in the highly seasonal Alpine ecosystem of Sierra Nevada Natural Space (SNNS), southern Spain.

Bottom-up regulation was found to only occur in healthy ibexes; the condition of infected ibexes was independent of primary productivity and snow cover. No link between ibex abundance and ibex body condition could be established when only considering infected individuals.

The pernicious effects of mange on Iberian ibexes overcome the benefits of favorable environmental conditions. Even though the increase in primary production exerts a positive effect on the body condition of healthy ibexes, the scabietic individuals do not derive any advantage from increased resource availability. Further applied research coupled with continuous sanitary surveillance are needed to address remaining knowledge gaps associated with the transmission dynamics and management of sarcoptic mange in free-living populations.

Keywords *Capra pyrenaica*, density-dependence, host-parasite relationships, Iberian Ibex, mountain ungulates, NDVI, remote sensing, *Sarcoptes scabiei*

5.1. Introduction

Body condition, *i.e*. energetic state and fat stores of an animal, is a major determinant of individual performance in most vertebrate species (Green, 2001), including ungulates (Serrano *et al*., 2008). In particular, the increase of body condition in anticipation of food shortages is one of the most common mechanisms displayed by herbivores to prevent starvation in highly seasonal environments (Parker *et al*., 2009). Parasites typically have a deleterious effect on body condition, mainly because infected hosts try to reduce the intensity or length of infestation by allocating resources in the activation of the immune response; they may also try to alleviate the damages caused by the infestation by investing energy in tissue repair and detoxification (Råberg *et al*., 2009). Because of this, one can expect the energetic costs of infestation are more pronounced in periods of food shortage (Beldomenico *et al*., 2009). Sarcoptic mange caused by the mite *Sarcoptes scabiei* is an excellent study model to evaluate how parasites may interfere with the bottom-up regulation of body condition in wild mammals inhabiting highly seasonal ecosystems. This mite is responsible for severe epizootic disease outbreaks in a broad range of mammals, sometimes causing increases in mortality rates. Infected animals typically suffer from dramatic structural and functional changes in the skin, becoming listless, dehydrated, emaciated and eventually dying from the infestation (Pence & Ueckerman, 2002). Notwithstanding the increasing knowledge about the immune response (Mounsey *et al*., 2015) and pathology (Nimmervoll *et al*., 2013) of sarcoptic mange, little is known about the relationship between environmental conditions, mange severity and body condition. This topic is of particular importance for the management of the disease, as hosts facing hard environmental conditions could experience increased mange severity. The energetic demands on the host, coupled with the induced physiological changes, make this parasitic disease particularly worrying for free-living populations inhabiting such environments.

Iberian ibex (*Capra pyrenaica*) is a medium-sized endemic mountain ungulate commonly affected by sarcoptic mange (Pérez *et al*., 2002). Mange outbreaks can result in devastating short-term mortality of ibexes, as happened in the *Sierras de Cazorla, Segura y Las Villas* Natural Park, southern Spain, in

the late 80s. There, approximately 95 % of ibexes were killed by the parasite (Pérez *et al*., 2002). Since 1992, sarcoptic mange has become endemic in the ibex population of the Sierra Nevada Natural Space (SNNS, hereafter). One particularity of this extreme Alpine ecosystem is the strong seasonal climatic variation found in the area, with snow cover present for six months of the year. SNNS ibex are adapted to such contrasted conditions and do display an income breeder strategy, *i.e*. increasing adipose tissues during the summer in anticipation of food deprivation during winter times (Serrano *et al*., 2011).

Previous studies have addressed the consequences of mange infestation in SNNS Iberian ibex population: *e.g*. immune response to first and second exposures (Sarasa *et al*., 2010), effects on individual growth (Serrano *et al*., 2007), reproductive allocation (Sarasa *et al*., 2011) and seasonal variation of hematology and biochemistry among scabietic ibexes (Pérez *et al*., 2015). To date, however, no information exists on how climatic conditions, vegetation dynamics and mange severity impact the body condition of these free-ranging ibexes. Although body weight reduction is detectable at early stages of infestation (Pérez *et al*., 2015), 80 % of ibexes recover totally from mange (Alassad *et al*., 2013). Thus, we can hypothesize that aside from the individual factors that shape resistance to *Sarcoptes scabiei* infestation, the effects of sarcoptic mange on ibex body condition will be influenced by the local environmental conditions (*e.g*. food availability, winter harshness) experienced during infestation.

Taking advantage of thirteen years (1995–2008) of data on sarcoptic mange monitoring in the Iberian ibex population of SNNS, we explored whether disease severity interacted with primary productivity, snow cover and ibex abundance in determining body condition. The strength of these interactions was assessed during two periods of contrasted vegetation dynamics and snow cover: green (March – October) and dormant period (November – February). We hypothesized that the deleterious effects of mange on ibex body condition will be compensated by favorable environmental conditions, *e.g*. high primary productivity, little snow cover and low population abundance. To the best of our knowledge, this study provides the first explicit assessment of how a parasitic disease shapes bottom-up processes in a large mammal.

5.2. Material and methods

5.2.1. Study area

The SNNS covers an area of approximately 2.000 km^2 and is characterized by a heterogeneous orography, with an altitudinal range between 860 and 3.482 m.a.s.l. (**Figure 19**). According to the Köppen–Geiger classification system, the SNNS experiences a Mediterranean Subartic climate (Kottek *et al*., 2006). Annual average precipitation is about 600 mm (Pérez-Luque *et al*., 2014). Minimum and maximum average monthly temperatures vary between −5 °C in February and 17 °C in July, with pronounced summer drought. The average annual temperature decreases from 12 to 16 °C below 1.500 m to 0 °C above 3.000 m. Snow generally covers a significant part of the study area between December and May; vegetation growth mainly occurs between June and August. SNNP encompasses the largest and best-known population of Iberian ibex in Andalusia (Pérez *et al*., 2002).

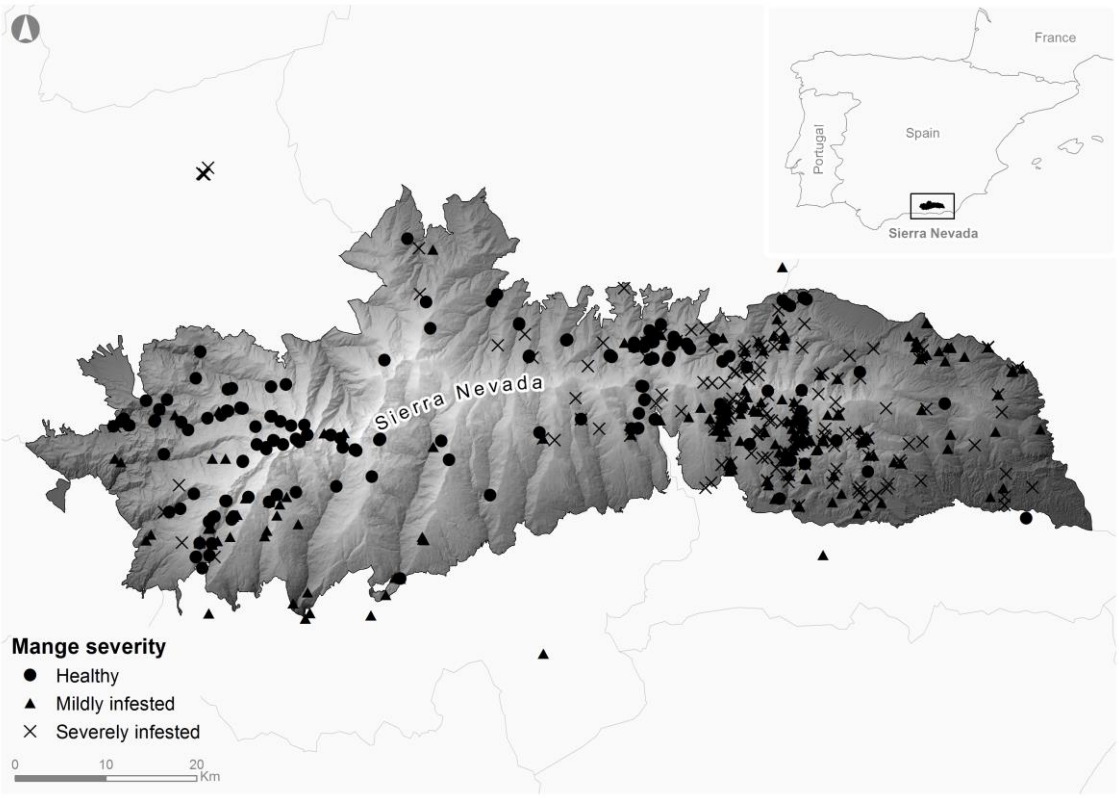

Figure 19. Location of the study area, the Sierra Nevada Natural Space. The spatial distribution of shot-harvested animals and the degree of mange severity (healthy, mildly and severely infested) are also showed.

5.2.2. Vegetation greenness and snow cover data

Two environmental variables were considered while assessing the role of bottom-up processes on the body condition of ibex: the normalized difference vegetation index (NDVI, **Figure 20**) used as a proxy of vegetation productivity, and snow cover (Myneni *et al*., 1997; Pettorelli *et al*., 2013). The former information was extracted from the MODIS repository (Moderate Resolution Imaging Spectroradiometer; http://modis.gsfc.nasa.gov) at a spatial resolution of 500 m and bi-monthly temporal resolution. Snow cover (percentage of surface covered by snow) was retrieved from the Observatorio Cambio Global - Sierra Nevada website (http://obsnev.es/linaria.html). Only NDVI values associated with shrubs and herbaceous layers were considered, since ibex primarily feed in areas encompassed by these landcover types in SNNS (Martínez, 2000). Mean monthly NDVI and snow cover values were computed for each year.

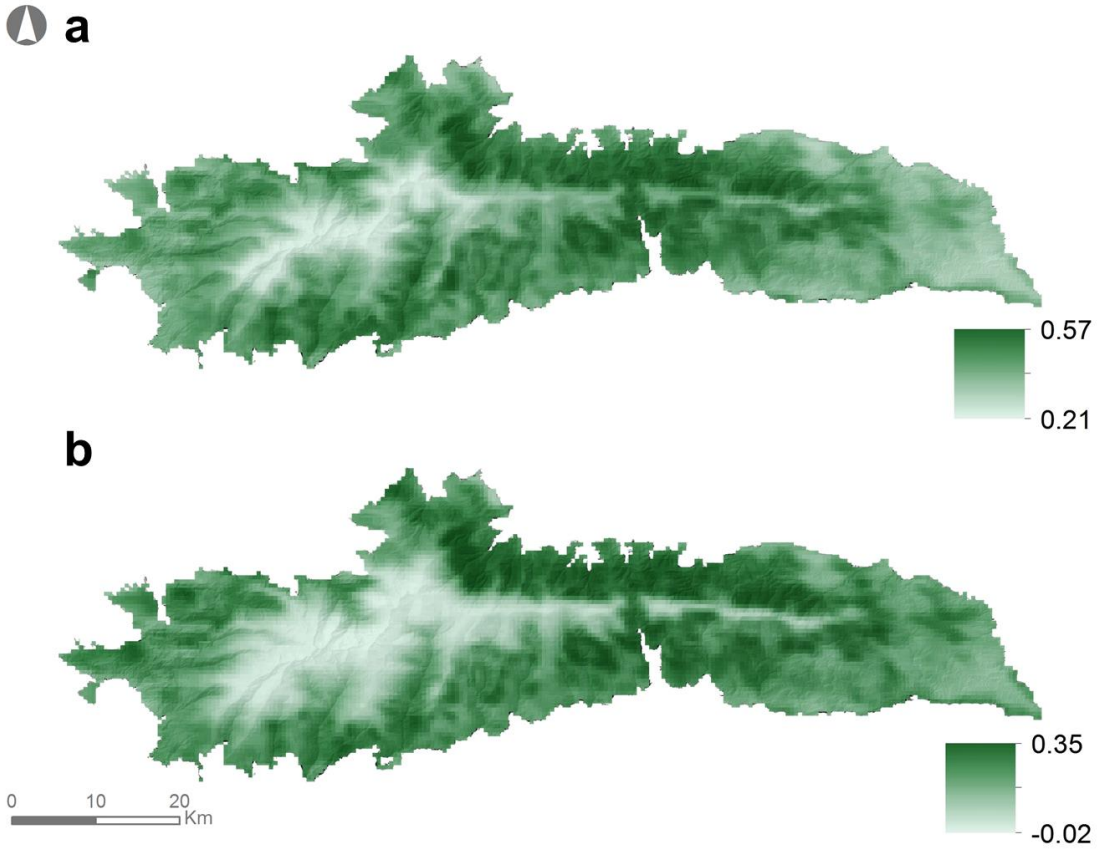

Figure 20. Spatial variability of NDVI during the **(a)** green (March – October) and **(b)** dormant (November – February) periods in the SNNS. Pixel values in each map correspond to the pixel average for the relevant season for the period 2000–2008**.**

5.2.3. Ibex data

We used block counts to estimate ibex abundance during the study period. In brief, a set of line transects were systematically placed in order to provide an equal coverage of habitats that occur in the study area. Thanks to this approach, the bias related to the systematic prospection of suitable areas was reduced. The survey was conducted every month by a fixed number of teams. Ibexes were observed by means of 8 × 40 binoculars and 20–60 × 65 spotting scopes. For modelling purposes, counts were expressed as the number of ibexes recorded in a given itinerary on a seasonal basis. A total of 243 male and 230 female Iberian ibexes older than two years were shot between 1995 and 2008, in the context of a mange control program carried out in the SNNS during this period. Sex was determined by visual inspection and the age in years was determined from horn-segment counts (Fandos, 1991). Mange severity was visually assessed using three categories, based on the percentage of skin surface affected by mites (Pérez *et al*., 2011b): healthy = ibexes without skin lesions, mildly infested = skin surface affected ≤ 50 % and severely infested when skin surface affected > 50 %. Animals were weighed to the nearest 0.1 kg; the kidneys were removed and transported to the laboratory in a cold box at 4 °C. Kidney fat reserves were assessed following Serrano *et al*. (2011) recommendations. Both fat-free kidney mass (KM) and associated peripheral fat (KF) are positively correlated to nutritional status and body condition of a wide range of mammals including Iberian ibex (Serrano *et al*., 2008). Therefore, we used the residuals from the linear regression between KM and KF as a proxy of body condition.

5.2.4. Statistical analyses

Partial least square regressions (PLSR) were used to assess the influence of disease severity, resource dynamics, intraspecific competition and snow cover on body condition. Carrascal *et al*. (2009) defined the PLSR method as an extension of multiple linear regressions in which a response variable (body condition) is modelled through the analysis of linear combinations among

predictors (NDVI, snow cover and ibex abundance). This technique is distribution free and well suited to handle multicollinearity issues, preventing possible misinterpretations of regression coefficients (Mevik & Wehrens, 2007). A PLSR model was developed for each combination of time period (green and dormant period) and mange severity (healthy, mildly and severely infested). Results are presented and interpreted under the assumption that body condition of severely infected ibexes is lower than in healthy animals and of those in early stages of infestation (López-Olvera *et al*., 2015). The sex of Iberian ibexes was excluded from the analysis because the lack of sex-biased effect of mange on ibexes' condition (López-Olvera *et al*., 2015). To minimize the potential effects of body growth on body condition, only individuals close to the final body size were retained in our analysis (≥3 years old (Fandos, 1991; Serrano *et al*., 2006). The significance of PLSR models was assessed through the Stone-Geisser Q^2 test, a cross-validation redundancy measure created to evaluate the predictive significance of the exogenous variables. Test values greater than 0.0975 indicate that the exogenous variables are statistically significant for the response, whereas values below this threshold reveal no significance. The R^2 was performed to measure the explanatory performance of models developed. Radar plots were used to explore the correlations between the variables and the first two axes associated to the first two components. All calculations were performed in *R* (version 3.2.0, *R* Development Core Team 2013). The package "*plspm*" was used to develop and visualize the PLSR outputs (Sanchez *et al*., 2015).

5.3. Results

Information on the body condition of 473 Iberian ibex was considered in our analyses: 43 (32 males and 11 females) of these individuals were classified as healthy, 217 (92 males and 125 females) as mildly infested and 213 (119 males and 94 females) as severely infested.

The monthly variations in the vegetation productivity, snow cover and ibex counts are shown in the **Figure 21**. As would be expected, vegetation productivity and snow cover were characterized by opposite trends. The

number of Iberian ibexes recorded a slight increase during the dormant period comprising the winter and the early spring.

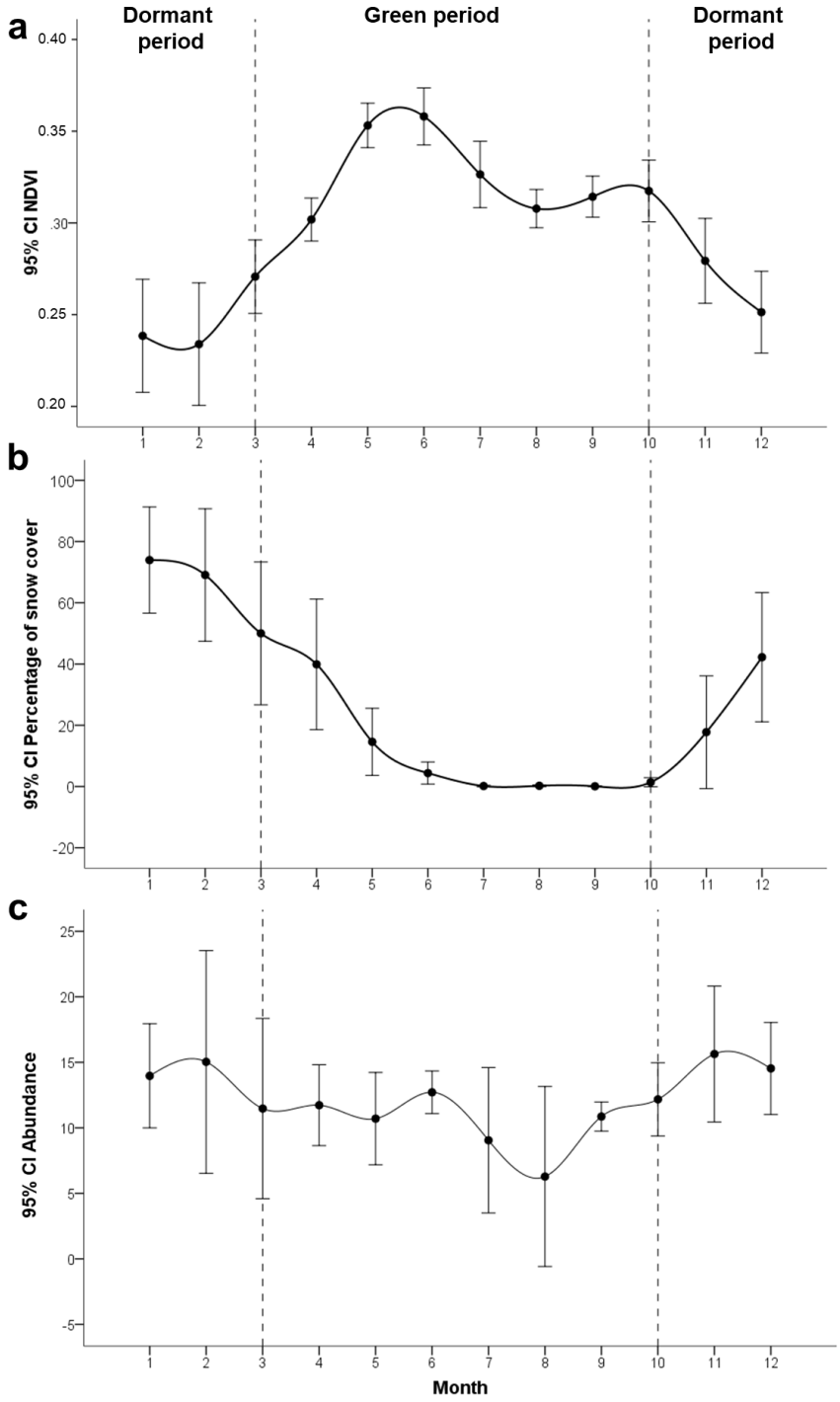

Figure 21. Intrannual variations of NDVI **(a)**, snow cover **(b)** and number of ibexes observed **(c)** in the SNNS. The error bars represent the inter-annual (1995–2008) fluctuations of variables values.

Summaries of PLSR analyses for each combination of time period and mange severity are presented in the **Tables 6** and **7**. Through Stone-Geyser's Q^2 test we identified that bottom-up regulations of ibex condition only occurred in healthy ibexes (Q^2 > 0.0975, **Table 6**). For healthy individuals, the considered environmental predictors as well as population abundance explained 25.14 % and 16.86 % of the observed variability in ibex body condition in the green and dormant period, respectively. Body condition of healthy animals was positively correlated with vegetation productivity (as indexed by average NDVI) and was negatively influenced by snow cover (**Figure 22**). Primary productivity (Load = 0.68, Weight = 0.62) and snow cover (Load = −0.71, Weight = −0.77) were the main drivers of body condition of healthy animals in the green period whereas the ibexes' abundance had greater relevance during the dormant season (Load = −0.62, Weight = −0.57) (**Table 7**, **Figure 23**). None of the environmental and population factors analyzed influenced body condition of diseased ibexes, either at the mild or severe mange stages of infestation (**Table 6**). Thus, neither higher primary productivity nor winter harshness and population abundance influenced the impact of mange on ibex body condition.

Table 6. R-squared and Stone-Geyser's Q^2 test values for the partial least squares regression (PLSR) analysis. Each model results from the combination between the two time-periods of contrasted vegetation productivity, and mange severity categories. A component is considered significant if $Q^2 \geq 0.0975$.

Period	Severity	R^2 (%)	Q^2
Green	Healthy	25.14	0.14
	Mildly infested	3.37	0.01
	Severely infested	0.2	-0.02
Dormant	Healthy	16.86	0.11
	Mildly infested	8.43	0.06
	Severely infested	0.01	-0.02

Table 7. Predictor weights and loads for the first component of partial least squares regression (PLSR) analysis. The contribution of each environmental predictor to the PLSR's axis X is represented by the predictor weights.

Period	Severity	Predictors	Loads	Weights
Green	Healthy	NDVI	0.68	0.62
		Snow	-0.71	-0.77
		Abundance	-0.35	-0.04
	Mildly infested	NDVI	-0.66	0.66
		Snow	0.55	0.25
		Abundance	0.60	0.70
	Severely infested	NDVI	0.67	0.59
		Snow	-0.65	0.75
		Abundance	-0.38	0.38
Dormant	Healthy	NDVI	0.59	0.55
		Snow	-0.52	-0.62
		Abundance	-0.62	-0.57
	Mildly infested	NDVI	-0.39	-0.29
		Snow	0.91	0.96
		Abundance	0.66	0.02
	Severely infested	NDVI	-0.62	-0.61
		Snow	0.42	0.36
		Abundance	0.67	0.70

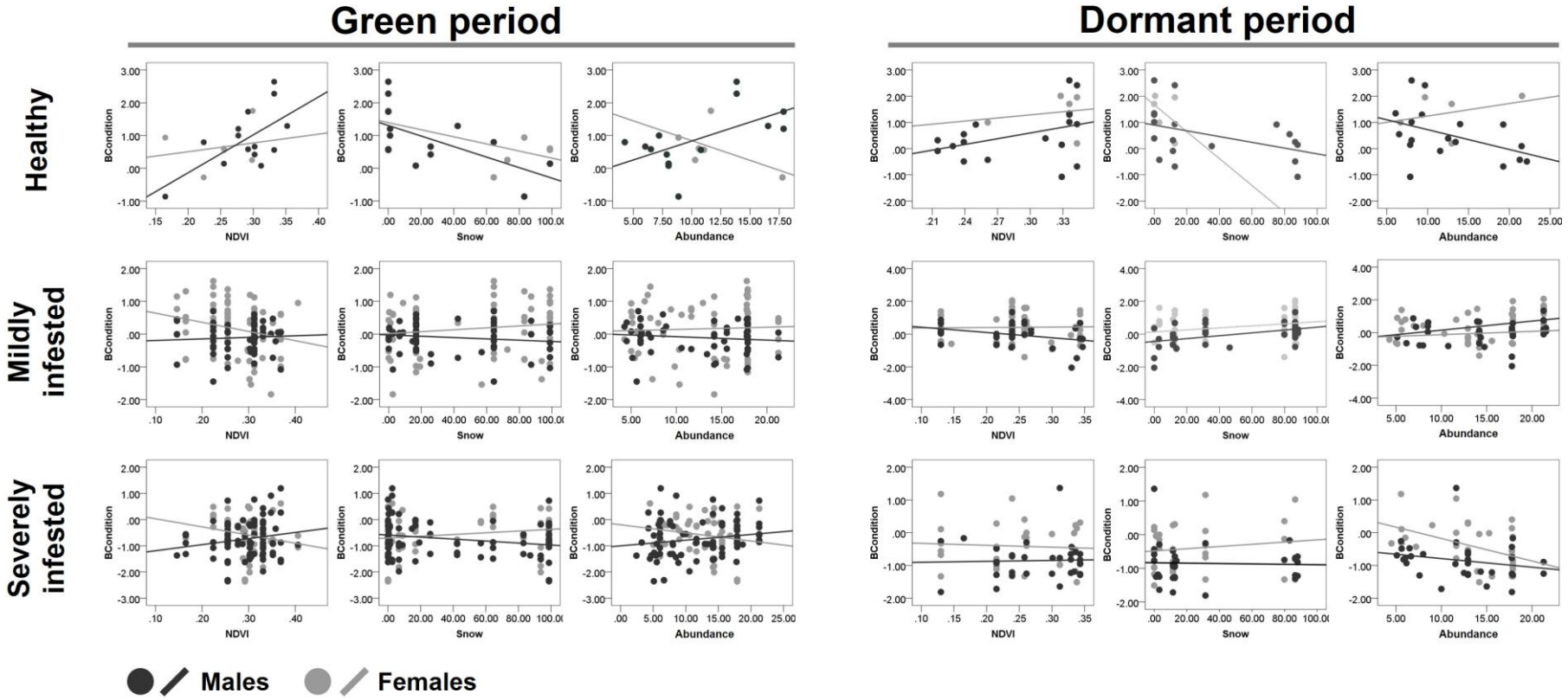

Figure 22. Relationship between body condition (males and females) and the three environmental predictors in healthy, mildly and severely infested animals across two time periods of contrasted vegetation productivity (green and dormant).

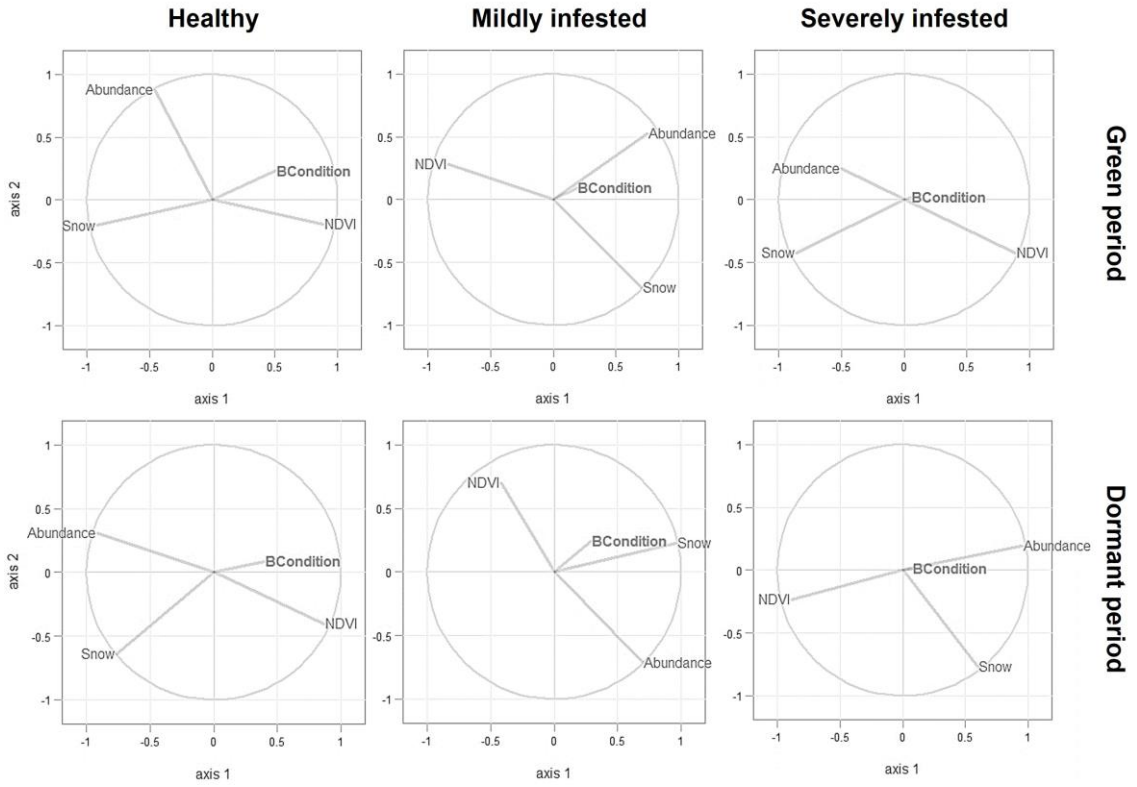

Figure 23. Correlation of the environmental predictors and the response with the first two partial least square regression (PLSR) components. Each segment represents a variable. Longer segments, *i.e*. closer to the perimeter of the circle, indicate that the corresponding variable has a higher weight in the PLSR component. Segments close to each other represent highly and positively correlated variables. On the other hand, segments in opposite extremes indicate a negative correlation. Orthogonal segments mean no correlation among predictors.

5.4. Discussion

This study provides the first known quantification of the impact of sarcoptic mange on the bottom-up regulation of body condition in a mountain ungulate. Our analyses led to three main results: i) an increase in primary productivity clearly triggers an increase in body condition in healthy ibexes, ii) sarcoptic mange can disrupt the link between environmental conditions and body condition, and iii) body condition is independent from ibex abundance parameter in scabietic ibexes.

The absence of a bottom-up regulation of body condition in scabietic individuals may be related to the physiopathology of this parasitic disease,

which is characterized by emaciation, muscle mass losses and anemia (Pence & Ueckerman, 2002; Bornstein *et al*., 2001). Even at the early/mild stages of infestation, mange can result in anemia (*i.e*. RBC, Hb, hematocrit reduction), accelerating the net catabolism of the body protein storage in ibex (*i.e*. increased blood urea and decreased creatine concentration) (Pérez *et al*., 2015). Such pathological and physiological changes have been reported in several other species inhabiting a wide range of environments (coyotes (*Canis latrans*), (Pence *et al*., 1983); rabbits (*Oryctolagus cuniculus*), (Arlian *et al*., 1988); red foxes (*Vulpes vulpes*), (Little *et al*., 1998); wombats (*Vombatus ursinus*), (Skerratt *et al*., 1999). For instance, Skerrat *et al*. (1999) showed that wombats were using their body stores to cope with the energetic costs of sarcoptic mange. Likewise, Arlian *et al*. (1988) concluded that the energy demand in rabbits is driven by mange severity *i.e*. severity increases the energetic costs to handle weight loss. These costs probably hinder the restoration of energy reserves in scabietic ibexes with severe hyperkeratotic lesions. However, in Iberian ibex the negative effects of sarcoptic mange on the capability to restore reserves was also present in the mildly stages of the disease. Indeed, sarcoptic mange exerts a negative and seasonal effect on body weight of infested Iberian ibexes (Pérez *et al*., 2015), compromising the daily weight gain.

When overabundance coincides with limited food availability, the ability of the hosts to cope with infestations can be compromised (Gortázar *et al*., 2006). Here, we failed to detect density-dependence in the bottom-up regulation of body condition in scabietic ibexes (see also Fernández- Morán *et al*. (1997) who reported the absence of correlation between host population density and mange prevalence in Cantabrian chamois (*Rupicapra pyrenaica parva*)). It has been suggested that host's abundance predisposes the population to mange infestation (Rossi *et al*., 1995; Oleaga *et al*., 2008), since host-to-host transmission is favored in crowded host populations (Alasaad, *et al*., 2013; León-Vizcaíno *et al*., 1999). In fact, aggregation improves disease maintenance (Rossi *et al*., 2005) and host susceptibility increase when high host densities coincide with limited food availability (Beldomenico *et al*., 2009). Despite all these evidences, once infected, food shortage due to intra-specific competition appears to have no effect on the body condition of infected individuals.

In healthy ibexes, the negative relationship between population abundance and body condition is less pronounced in the green period than in the dormant season. This result could be explained by the habitat use of Iberian ibex. As with other closely related *Caprinae* species (Grignolio *et al*., 2003), ibexes can be easily seen around alpine meadows and pastures looking for sites free from snow and with fresh vegetation. However, during the dormant period the strong and negative relationship between population abundance and body condition can be explained by the fact that available resources are probably not sufficient to cover ibex' energetic needs. Such a period also coincides with a reduction of forage intake and the typical increase of energy expenditure due to rut (Brivio *et al*., 2010). Therefore, whereas food shortage in the dormant period would act as a classical population bottom-up regulator, higher food availability during the high production green period would allow the Iberian ibex population to thrive.

Here, we have shown how scabietic ibexes do not take advantage of increases in resource availability, which is a drawback to the implementation of management practices, at least in the short term. A very recent work underlined the ability of ibexes to survive from mange infestation, which opens a new window to disease management (Alasaad *et al*., 2013). Further research should be focused on the effects of habitat management on the progression of mange and the survival of scabietic individuals.

CHAPTER 6 Major findings and conclusions

* The highest summits of Sierra Nevada. The peak *Mulhacén*, to the right, is the highest point of the Iberian Peninsula (3.482 m.a.s.l.). Photo: João Carvalho.

The conservation and management of wild ungulates should be set on a holistic framework, under the umbrella of disease, hybridization, habitat loss and sustainable harvesting. Over the last decades, translocation initiatives and protection allowed the recovery of Iberian ibex populations, and scientific cooperation increased our knowledge about the species dynamics and threats. All these efforts will be irrelevant if policy makers and game managers do not consider the results gathered from applied ecological research. This final chapter provides an overview of the main results and summarizes the key findings of the thesis.

Three general hypotheses supported this thesis. The first hypothesis stated that diet quality and composition could be tracked using cost-effective tools, such as satellite vegetation indices. Chapter 2 did not provide clear scientific evidences to support this hypothesis. The second hypothesis established that horn growth patterns and trends are shaped by the interactive effects of selective pressures. This hypothesis was supported by the studies presented in the Chapter 3 and 4. Finally, it was hypothesized that favorable environmental conditions mitigate the negative effects of disease on body condition. Chapter 5 did not confirm this working hypothesis.

The chapter 2 aimed to characterize the diet quality and composition of male ibexes and to explore a cost-effective methodology able to predict the dietary features of Mediterranean Iberian ibex population.

Major findings

- Diet quality and composition of wild ibexes follow a seasonal pattern;
- FN picked in the spring, while fibers picked in the winter. The consumption of non-leguminous woody species was higher in the winter, while leguminous woody species and forbs were more representative in the spring;
- Both nutritional indicators, diet quality and composition, are related. Seasonality shapes this relationship;
- Satellite vegetation indexes, such as NDVI, did not always coincide with increased fecal nitrogen and did not relate with diet composition.

Conclusions and management implications

- Fecal indicators are good alternatives to direct forage surveys;
- The use of satellite-based products as proxies of the diet quality of wild ungulates inhabiting highly heterogeneous habitats must be done with caution;
- Imaging spectroscopy, with fine spatial and spectral resolution, should be tested in Mediterranean ecosystems as an alternative to: (i) link nutritional requirements of wild ungulates to resources availability and quality; (ii) parametrize resource maps; and (iii) estimate the carrying capacity of Mediterranean habitats.

The chapter 3 was aimed at investigating the horn growth patterns of male ibexes and the possibility of male individuals present the mechanism of compensatory horn growth.

Major findings

• Nearly a quarter of variation in annual segments was explained by individual heterogeneities;

• Habitat characteristics fostered significant horn growth differences, *i.e*. the annual segments of males living in open areas of shrubs and meadows were significantly longer than the segments of those males living in forest-dominated areas;

• Compensatory or fine-scale compensatory horn growth was not recorded for this species, independently of the habitat type and cohort.

Conclusions and management implications

• Spatial heterogeneities in habitat characteristics are key for among-individual differences in horn growth;

• The horn growth at young ages are a reliable proxy of horn size at older ages, *i.e*. fast-growing and large-horned young males are likely to become large-horned mature males;

• The absence of compensatory horn growth makes the species more prone to suffer from the potential evolutionary and/or phenotypic effects from trophy hunting;

• The absence of fine-scale compensatory horn growth means that a single year of nutritional deficits could constrain the phenotypic potential of an entire cohort;

• The study of other horn parameters (*e.g*. segment volume) will be important to gather conclusive remarks regarding the occurrence of compensatory horn growth.

The chapter 4 was focused on determining the factors (local weather conditions, habitat structure, density-dependence and hunting strategy) underlying the long-term decrease of horn size.

Major findings

• Factors related to habitat structure and hunting strategy accounted for the variation in length of annual segments, *i.e*. while pine forest encroachment had a negative effect on annual horn growth, the selective offtake of undesirable phenotypes had a positive effect;

• Local weather conditions and population size did not influence annual horn growth.

Conclusions and management implications

• The forest encroachment of open meadows and heterogeneous grasslands limits the horn growth of male ibexes, probably due to dietary shifts, nutritional deficits and an increasing competition for resources;

• Management measures aimed at increasing preferred habitats (*e.g*. logging and thinning of forest patches) and the productivity of forage (*e.g*. prescribed fire) must be on the game managers agenda;

• An adaptative management is necessary to increase the resilience of shrublands and grasslands to expected scenarios of land abandonment and Mediterranean drought;

• No effect of trophy hunting on horn growth was detected, however it could take several generations to be perceptible. The creation of harvest refuges and the protection of fast-growing and large-horned younger males could be important to neutralize the undesirable consequences of trophy hunting.

The study area in chapters 2, 3 and 4 were in *Els Ports de Tortosa i Beseit*, northeastern Spain. The chapter 3 and 4 are a good example that long-term studies are dynamic, lead to new hypothesis and allow to refine previous findings.

The chapter 5 assessed how temporal variation in climatic conditions, vegetation dynamics, population density, and sarcoptic mange impacted the body condition of Iberian ibexes inhabiting the highly seasonal ecosystem of *Sierra Nevada*, southern Spain.

Major findings

• The vegetation productivity (as indexed by average NDVI) had a positive effect on the body condition of healthy ibexes;

• The vegetation productivity and snow cover driven body condition of healthy ibexes during the green-up period (March – October), whereas density-dependent effects had greater relevance during the dormant period (November – February);

• Environmental and population factors had no influence on the body condition of mildly and severely infested ibexes, which suggests that sarcoptic mange breaks up the bottom-up regulation of body condition.

Conclusions and management implications

• The negative effects of population density on the body condition of healthy ibexes suggests that available resources are not enough to fill ibex needs;

• The pernicious effects of sarcoptic mange on the body condition of ibexes overcome the positive effects derived from favorable environmental conditions;

• The disruption of bottom-up regulation of body condition by sarcoptic mange is expected to have an indirect impact on the development of secondary sexual characters, such as horns;

• Further research is needed to establish a direct link between disease and the development of phenotypic traits.

Overall, this thesis shows the importance of data collected from hunted animals for wildlife research and represents an important contribution to understand the effects of size-selective harvesting, environmental variation and diseases on the life-history traits of Iberian ibex. While important advancements have been achieved on many topics related with the management of wild Iberian ibex populations, strategic future efforts should be weighted towards an adaptative management. This exercise is crucial to anticipate the impacts of environmental changes on species life-history traits and to guarantee the sustainability of trophy hunting.

It is important to:

• Determine and standardize precise and cost-effective methods of population assessment (*e.g*. population size and density, nutritional and health condition);

• Define consistent metrics regarding the carrying capacity of natural Mediterranean habitats;

• Track individuals and social groups living under different ecological scenarios and across their life spans. This could be of particular interest for translocated individuals and new population nucleus;

• Record growth and genetic data from marked individuals on a regular basis and/or, at least, the measure of horn growth segments from harvested males, as it reflects short-term environmental fluctuations.

This will help to increase the understanding of several topics related to fundamental ecology, but also allows to address particular conservation and sustainability issues. We should be able to:

• Increase our understanding on the effects of human-induced and/or environmental changes on phenotypic traits variation;

• Quantify the effects of variable nutrition and dietary restrictions on secondary sexual characters, such as horn growth;

• Assess the parental effects on the phenotypic expression of an individual (establish a pedigree and assign paternity);

• Detect silver spoon effects, *i.e*. evaluate if early-life environmental conditions impact the individual performance later in life;

• Understand how available energetic resources are balanced between opposing expenditures (*e.g*. horn growth versus body mass);

• Disentangle if trait changes are due to genetic effects or phenotypic plasticity and analyze how phenotypic plasticity drive evolutionary trajectories;

• Describe the way environmental conditions are influencing the gene expression (epigenetics);

• Determine breeding values and evaluate if breeding success is driven by specific traits (*e.g*. evaluate to what extent horn size contributes to male reproductive success);

• Explore if well-developed males have particular genetic characteristics that make them more resistant and resilient to habitat deterioration, density-dependency and diseases;

• Evaluate if translocations are a good alternative to dilute the effects of inbreeding depression through gene flow;

• Quantify the role of individual heterogeneity on population dynamics.

These important questions demand deeper scrutiny; however, they are data-dependent and require a serious long-term commitment of policy makers, game managers and wildlife researchers. Life-history strategies and traits may vary among populations and among individuals within a population for different reasons and at different time scales. We therefore advocate the creation of a research network, that extends over neighboring populations and beyond artificial management units. Looking toward the future of trophy hunting, the establishment of this network and the answer to the abovementioned points will provide the scientific support to mitigate potential threats resulting from intense selective harvesting and environmental changes.

References

Acevedo, P. & Cassinello, J. (2009). Biology, ecology and status of Iberian ibex *Capra pyrenaica*: a critical review and research prospectus. Mammal Review, 39, 17-32.

Acevedo, P., Cassinello, J. & Gortázar, C. (2007a). The Iberian ibex is under an expansion trend but displaced to suboptimal habitats by the presence of extensive goat livestock in central Spain. Biodiversity and Conservation, 16, 3361-3376.

Acevedo, P., Cassinello, J., Hortal, J. & Gortázar, C. (2007b). Invasive exotic aoudad (*Ammotragus lervia*) as a major threat to native Iberian ibex (Capra pyrenaica): a habitat suitability model approach. Diversity and Distributions, 13, 587-597.

Acevedo, P., Farfán, M.A., Márquez, A.L., Delibes-Mateos, M., Real, R. & Vargas, J.M. (2011). Past, present and future of wild ungulates in relation to changes in land use. Landscape Ecology, 26, 19-31.

Akaike, H. (1974). A new look at the statistical model identification. IEEE Transactions on Automatic Control, 19, 716-723.

Alasaad, S., Granados, J.E., Fandos, P., Cano-Manuel, F.J., Soriguer, R.C. & Pérez, J.M. (2013). The use of radio-collars for monitoring wildlife diseases: a case study from Iberian ibex affected by *Sarcoptes scabiei* in Sierra Nevada, Spain. Parasites & Vectors, 6, 242.

Albon, S.D. & Langvatn, R. (1992). Plant phenology and the benefits of migration in a temperate ungulate. Oikos, 65, 502-513.

Allendorf, F.W. & Hard, J.J. (2009). Human-induced evolution caused by unnatural selection through harvest of wild animals. Proceedings of the National Academy of Sciences, 106, 9987-9994.

Álvarez, F. (1990). Horns and fighting in male Spanish ibex, *Capra pyrenaica*. Journal of Mammalogy, 71, 608-616.

Apollonio, M., Andersen, R. & Putman, R. (2010). European Ungulates and their Management in the 21st Century. Cambridge University Press, New York.

Arlian, L.G., Ahmed, M. & Vyszenski-Moher, D.L. (1988). Effects of *S. scabiei* var. *canis* (Acari: Sarcoptidae) on blood indexes of parasitized rabbits. Journal of Medical Entomology, 25, 360-369.

Barboza, P.S., Parker, K.L. & Hume, I.D. (2009). Integrative Wildlife Nutrition. Springer, Berlin.

Bartolomé, J., Franch, J., Gutman, M. & Seligman, N.G. (1995). Technical Note: Physical factors that influence fecal analysis estimates of herbivore diets. Journal of Range Management, 48, 267-270.

Barton, K. (2015). MuMIn: Multi-model inference. R Package Version 1.42.1. http://CRAN.R-project.org/package=MuMIn.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., … Green, P. (2018). lme4: Linear Mixed-Effects Models using 'Eigen' and S4. R Package Version 1.1-17. https://cran.r-project.org/web/packages/lme4/index.html.

Beldomenico, P.M. & Begon, M. (2009). Disease spread, susceptibility and infestation intensity: vicious circles? Trends in Ecology and Evolution, 25, 21–27.

Bell, R.H.V. (1971). A grazing ecosystem in the Serengeti. Scientific American, 225, 86-89.

Bergeron, P., Festa-Bianchet, M., Von Hardenberg, A. & Bassano, B. (2008). Heterogeneity in male horn growth and longevity in a highly sexually dimorphic ungulate. Oikos, 117, 77-82.

Bishop, C.J., Unsworth, J.W. & Garton, E.O. (2005). Mule deer survival among adjacent populations in southwest Idaho. The Journal of Wildlife Management, 69, 311-321.

Bornstein, S., Mörner, T. & Samuel, W.M. (2001). *Sarcoptes scabiei* and sarcoptic mange. In: Samuel, W.M., Pybus, M.J. & Kocan, A.A. (Eds.), Parasitic Diseases of Wild Mammals, Second ed. Iowa State University Press, Ames. pp. 107-119.

Borowik, T., Pettorelli, N., Sönnichsen, L. & Jędrzejewska, B. (2013). Normalized difference vegetation index (NDVI) as a predictor of forage availability for ungulates in forest and field habitats. European Journal of Wildlife Research, 59, 675-682.

Boyce, M.S. & Krausman P.R. (2018). Controversies in mountain sheep management. The Journal of Wildlife Management, 82, 5-7.

Brivio, F., Grignolio, S. & Apollonio, M. (2010). To feed or not to feed? Testing different hypotheses on rut-induced hypophagia in a mountain ungulate. Ethology, 115, 1-10.

Bueno, C.G., Barrio, I.C., García-González, R., Alados, C.L. & Gómez-García, D. (2010). Does wild boar rooting affect livestock grazing areas in alpine grasslands? European Journal of Wildlife Research, 56, 765-770.

Bunnell, F.L. (1978). Horn growth and population quality in Dall sheep. The Journal of Wildlife Management, 42, 764-775.

Büntgen, U., Galván, J.D., Mysterud, A., Krusic, P.J., Hülsmann, L., Jenny, H., … Bollman, K. (2018). Horn growth variation and hunting selection of the Alpine ibex. Journal of Animal Ecology, 87, 1069-1079.

Büntgen, U., Krusic, P.J., Verstege, A., Sangüesa-Barreda, G., Wagner, S., Camarero, J., … Esper, J. (2017). New tree-ring evidence from the Pyrenees reveals western Mediterranean climate variability since Medieval times. Journal of Climate, 30, 5295-5318.

Büntgen, U., Liebhold, A., Jenny, H., Mysterud, A., Egli, S., Nievergelt, D., … Bollmann, K. (2014). European springtime temperature synchronises ibex horn growth across the eastern Swiss Alps. Ecology Letters, 17, 303-313.

Burnham, K.P. & Anderson, D.R. (2002). Model Selection and Multimodel Inference: a Practical Information-theoretic Approach, Second ed. Springer-Verlag, New York.

Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., … Richardson, A.J. (2011). The pace of shifting climate in marine and terrestrial ecosystems. Science, 334, 652-655.

Burton, T. & Metcalfe, N.B. (2014). Can environmental conditions experienced in early life influence future generations? Proceedings of the Royal Society of London B: Biological Sciences, 281, 20140311.

Cabral, M.J., Almeida, J., Almeida, P.R., Delliger, T., Ferrand de Almeida, N., Oliveira, M.E., ... Santos-Reis, M. (2005). Livro Vermelho dos Vertebrados de Portugal. Instituto da Conservação da Natureza, Lisboa.

Cabrera, A. (1911). The subspecies of the Spanish Ibex. Proceedings of the Zoological Society of London, LXVI, 963-977.

Carrascal, L.M., Galván, I. & Gordo, O. (2009). Partial least squares regression as an alternative to current regression methods used in ecology. Oikos, 118, 681-690.

Carvalho, J., Eizaguirre, O., Pérez, J.M., Mentaberre G., Lavín, S., Fandos, P., ... Serrano, E. (2017). Evidence for phenotypic plasticity but not for compensatory horn growth in male Iberian ibex. Mammalian Biology, 87, 101-106.

Carvalho, J., Torres, R.T., Acevedo, P., Santos, J.P.V., Barros, T., Serrano, E. & Fonseca, C. (2018). Propagule pressure and land cover changes as main drivers of red and roe deer expansion in mainland Portugal. Diversity and Distributions, 24, 551-564.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., … Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. Science, 346, 1517-1519.

Chirichella, R., Ciuti, S., Grignolio, S., Rocca, M. & Apollonio, M. (2013). The role of geological substrate for horn growth in ungulates: a case study on Alpine chamois. Evolutionary Ecology, 27, 145-163.

Cho, M.A. & Skidmore, A.K. (2009). Hyperspectral predictors for monitoring biomass production in Mediterranean mountain grasslands: Majella National Park, Italy. International Journal of Remote Sensing, 30, 499-515.

Christianson, D. & Creel, S. (2009). Fecal chlorophyll describes the link between primary production and consumption in a terrestrial herbivore. Ecological Applications, 19, 2009, 1323-1335.

Clouet, M. (1979). Note sur la systématique du bouquetin d'Espagne. Bulletin de la Société d'histoire naturelle de Toulouse, 115, 269-277.

Clutton-Brock, T., Iason, G.R. & Guinness, F.E. (1987). Sexual segregation and density-related changes in habitat use in male and female red deer (*Cervus elaphus*). Journal of Zoology, 211, 275-289.

Clutton-Brock, T. & Sheldon, B.C. (2010). Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology and Evolution, 25, 562-573.

Codron, D., Lee-Thorp, J.A., Sponheimer, M, & Codron, J. (2007). Nutritional content of savanna plant foods: implications for browser/grazer models of ungulate diversification. European Journal of Wildlife Research, 53, 100-111.

Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C. & Festa-Bianchet, M. (2003). Undesirable evolutionary consequences of trophy hunting. Nature, 426, 655-658.

Cook, R.C., Cook, J.G., Vales, D.J., Johnson, B.K., McCorquodale, S.M., Shipley, L.A., … Schmitz, L. (2013). Regional and seasonal patterns of nutritional condition and reproduction in elk. Wildlife Monograph, 184, 1-45.

Corlatti, L., Gugiatti, A. & Imperio, S. (2015). Horn growth patterns in Alpine chamois. Zoology, 118, 213-219.

Côté, S.D., Festa-Bianchet, M. & Smith, K.G. (1998). Horn growth in mountain goats (*Oreamnos americanus*). Journal of Mammalogy, 79, 406-414.

Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C. & Waller, D. M. (2004). Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics, 35, 113-147.

Coulson, T., Schindler, S., Traill, L. & Kendall., B.E. (2018). Predicting the evolutionary consequences of trophy hunting on a quantitative trait. The Journal of Wildlife Management, 82, 46-56.

Creech, T.G., Epps, C.W., Monello, R.J. & Wehausen, J.D. (2016). Predicting diet quality and genetic diversity of a desert-adapted ungulate with NDVI. Journal of Arid Environments, 127, 160-170.

Cromsigt, J.P.G.M., Kuijper, D.P.J., Adam, M., Beschta, R.L., Churski, M., Eycott, A., … West, K. (2013). Hunting for fear: innovating management of human–wildlife conflicts. Journal of Applied Ecology, 50, 544-549.

Crosmary, W.-G, Loveridge, A.J., Ndaimani, H., Lebel, S., Booth, V., Côte, S.D. & Fritz, H. (2013). Trophy hunting in Africa: long-term trends in antelope horn size. Animal Conservation, 16, 648-660.

Danell, K., Duncan, P., Bergström, R. & Pastor, J. (2006). Large Herbivore Ecology, Ecosystem Dynamics and Conservation. Cambridge University Press, Cambridge.

Darimont, C.T., Carlson, S.M., Kinnison, M.T., Paquet, P.C., Reimchen, T.E. & Wilmers, C.C. (2009). Human predators outpace other agents of trait change in the wild. Proceedings of the National Academy of Sciences, 106, 952-954.

Demment, M.W. & Van Soest, P.J. (1985). A nutritional explanation for body size patterns of ruminant and nonruminant herbivores. American Naturalist, 125, 641-672.

Descamps, S., Gaillard, J.-M., Hamel, S. & Yoccoz, N.G. (2016). When relative allocation depends on total resource acquisition: implication for the analysis of trade-offs. Journal of Evolutionary Biology, 29, 1860-1866.

Di Minin, E., Leader-Williams, N. & Bradshaw, C.J.A. (2016). Banning trophy hunting will exacerbate biodiversity loss. Trends in Ecology and Evolution, 31, 99-102.

Diamond, J. (1997). Guns, Germs, and Steel: The Fates of Human Societies. Norton & Company, New York.

Dmitriew, C.M. (2011). The evolution of growth trajectories: what limits growth rate? Biological Reviews, 86, 97-116.

Douhard, M., Festa-Bianchet, M., Pelletier, F., Gaillard, J.-M. & Bonenfant, C. (2016). Changes in horn size of Stone's sheep over four decades correlate with trophy hunting pressure. Ecological Applications, 26, 309-321.

Douhard, M., Pigeon, G., Festa-Bianchet, M., Coltman, D.W., Guillemette, S. & Pelletier, F. (2017). Environmental and evolutionary effects on horn growth of male bighorn sheep. Oikos, 126, 1031-1041.

Duparc, A., Redjadj, C., Viard-Crétat, F., Lavorel, S., Austrheim, G. & Loison, A. (2013). Co-variation between plant above-ground biomass and phenology in sub-alpine grasslands. Applied Vegetation Science, 16, 305-316.

Escos, J. & Alados, C.L. (1992). The home-range of the Spanish ibex in spring and fall. Mammalia, 56, 57-63.

Ezenwa, V.O. & Jolles, A.E. (2008). Horns honestly advertise parasite infection in male and female African buffalo. Animal Behaviour, 75, 2013-2021.

Fandos, P. (1991). La cabra montés *Capra pyrenaica* en el Parque Natural de las Sierras de Cazorla. ICONA–CSIC, Segura y Las Villas, Madrid.

Fandos, P. (1995). Factors affecting horn growth in male Spanish ibex (*Capra pyrenaica*). Mammalia, 2, 229-235.

Fandos, P., Arcenegui, P., Lora, M.A., Buron, D., Granados, J.E. & Cadenas, R. (2010a). Evolución demográfica de la cabra montés en Andalucía en los últimos 100 años. Galemys, 22, 347-358.

Fandos, P., Arcenegui, P., Lora, M.A., Buron, D. & Cadenas, R. (2010b). Los trofeos de cabra montés (*Capra pyrenaica*) y la calidad cinegética. Galemys, 22, 331-345.

Feder, C., Martin, J.G.A., Festa-Bianchet, M., Bérubé, C. & Jorgenson, J. (2008). Never too late? Consequences of late birthdate for mass and survival of bighorn lambs. Oecologia, 156, 773-781.

Fenberg, P.B. & Roy, K. (2008). Ecological and evolutionary consequences of size-selective harvesting: how much do we know? Molecular Ecology, 17, 209-220.

Fernández-Morán, J., Gómez, S., Ballesteros, F., Quirós, P., Benito, J.L., Feliu, C. & Nieto, J.M. (1997). Epizootiology of sarcoptic mange in a population of cantabrian chamois (*Rupicapra pyrenaica parva*) in Northwestern Spain. Veterinary Parasitology, 73, 163-171.

Festa-Bianchet, M., Jorgenson, J.T., Lucherini, M. & Wishart. W.D. (1995). Life-history consequences of variation in age of primiparity in bighorn ewes. Ecology, 76, 871-881.

Festa-Bianchet, M. (2003). Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. In: Festa-Bianchet, M. & Apollonio, M. (Eds.), Animal Behavior and Wildlife Conservation. Island Press, Washington, D.C., pp. 191-207.

Festa-Bianchet, M., Coltman, D.W., Turelli, L. & Jorgenson, J.T. (2004). Relative allocation to horn and body growth in bighorn rams varies with resource availability. Behavioral Ecology, 15, 305-312.

Festa-Bianchet, M., Pelletier, F., Jorgenson, J.T., Feder, C. & Hubbs, A. (2014). Decrease in horn size and increase in age of trophy sheep in Alberta over 37 years. The Journal of Wildlife Management, 78, 133-141.

Festa-Bianchet, M. (2016). When does selective hunting select, how can we tell, and what should we do about it? Mammal Review, 47, 76-81.

Festa-Bianchet, M., Douhard, M., Gaillard, J.-M. & Pelletier, F. (2017). Successes and challenges of long-term field studies of marked ungulates. Journal of Mammalogy, 98, 612-620.

Fonseca, C., Carvalho, J., Santos, J.P.V., Torres, R.T. & Bencatel, J. (2017). Artiodáctilos. In: Bencatel, J., Álvares, F., Moura, A.E. & Barbosa, A.M. (Eds.), Atlas de Mamíferos de Portugal. Universidade de Évora, Évora, pp. 98-111.

Fonseca, C., Migueis, D., Fernandes, T., Carvalho, H., Loureiro, A., Carvalho, J. & Torres, R.T. (2017). The return of the Iberian wild goat *Capra pyrenaica* to Portugal: From reintroduction to recolonization. Journal for Nature Conservation, 38, 56-61.

Fritz, H., Loreau, M., Chamaillé-Jammes, S., Valeix, M. & Clobert, J. (2011). A food web perspective on large herbivore community limitation. Ecography, 34, 196-202.

Gálvez-Cerón, A., Serrano, E., Bartolomé, J., Mentaberre, G., Fernández-Aguilar, X., Fernández-Sirera, L., ... Albanell, E., (2013). Predicting seasonal and spatial variations in diet quality of Pyrenean chamois (*Rupicapra pyrenaica pyrenaica*) using near infrared reflectance spectroscopy. European Journal of Wildlife Research, 59, 115-121.

Gálvez-Cerón, A., Gassó, D., López-Olvera, J.R., Mentaberre, G., Bartolomé, J., Marco,I., ... Serrano, E., (2015). Gastrointestinal nematodes and dietary fibre: two factors to consider when using FN for wildlife nutrition monitoring. Ecological Indicators, 52, 161-169.

Garel, M., Cugnasse, J.M., Maillard, D., Gaillard, J.-M., Hewison, A.J. & Dubray, D. (2007). Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. Ecological Applications, 17, 1607-1618.

Geist, V. (1966). The evolution of horn-like organs. Behaviour, 27, 175-214.

Gendreau, Y., Côté, S.D. & Festa-Bianchet, M. (2005). Maternal effects on post-weaning physical and social development in juvenile mountain goats (*Oreamnos americanus*). Behavioral Ecology and Sociobiology, 58, 237-246.

Giacometti, M., Willing, R. & Defila, C. (2002). Ambient temperature in spring affects horn growth in male Alpine ibexes. Journal of Mammalogy, 83, 245-251.

Gordon, I.J., Hester,A.J. & Festa-Bianchet, M. (2004). The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology, 41, 1021-1031.

Gortázar, C., Acevedo, P., Ruiz-Fons, F. & Vicente, J. (2006). Disease risks and overabundance of game species. European Journal of Wildlife Research, 52, 81-87.

Granados, J.E., Pérez, J.M., Márquez, F.J., Serrano, E., Soriguer, R.C. & Fandos, P. (2001). La cabra montés (*Capra pyrenaica*, Schinz 1838). Galemys, 13, 3-37.

Granados, J.E., Soriguer, R.C., Pérez, J.M., Fandos, P. & García, J. (2007). *Capra pyrenaica* Schinz, 1838. In: Palomo, L.J., Gisbert, J. & Blanco, J.C. (Eds.). Atlas y Libro Rojo de los Mamíferos Terrestres de España. Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid, pp. 366-368.

Granados, M.E., Vilagrosa, A., Chirino, E. & Vallejo, V.R. (2016). Reforestation with resprouter species to increase diversity and resilience in Mediterranean pine forests. Forest Ecology and Management, 362, 231-240.

Green, A.J. (2001). Mass/length residuals: measures of body condition or generators of spurious results? Ecology, 82, 1473-1483.

Grignolio, S., Parrini, F., Bassano, B., Luccarini, S. & Apollonio, M. (2003). Habitat selection in adult males of Alpine ibex, *Capra ibex ibex*. Folia Zoologica, 52, 113-120.

Hamel, S., Côté, S.D. & Festa-Bianchet, M. (2010). Maternal characteristics and environment affect the costs of reproduction in female mountain goats. Ecology, 91, 2034-2043.

Hamel, S., Gaillard, J.-M., Yoccoz, N.G., Albon, S., Côté, S.D., Craine, J.M., ... Tveraa, T. (2016). Cohort variation in individual body mass dissipates with age in large herbivores. Ecological Monographs, 86, 517-543.

Hamel, S., Garel, M., Festa-Bianchet, M., Gaillard, J.M. & Côté, S.D. (2009). Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. Journal of Applied Ecology, 46, 582-589.

Harder, J.D. & Kirkpatrick, R.L. (1994). Physiological methods in wildlife research. In: Bookhout, T.A. (Ed.), Research and Management Techniques for Wildlife and Habitats, Fifth ed. The Wildlife Society, Bethesda, pp. 275-306.

Hedrick, P.W. (2011). Rapid decrease in horn size of bighorn sheep: environmental decline, inbreeding depression, or evolutionary response to trophy hunting? Journal of Heredity, 102, 770-781.

Heffelfinger, J.R. (2018a). Inefficiency of evolutionarily relevant selection in ungulate trophy hunting. The Journal of Wildlife Management, 82, 57-66.

Heffelfinger, J.R. (2018b). Obstacles to evolutionary consequences of ungulate trophy hunting: Reply to Kardos *et al*. The Journal of Wildlife Management, 82, 892-895.

Heimer, W.E. & Smith, A.C. (1975). Ram horn growth and population quality. their significance to Dall sheep management in Alaska. Wildlife Technical Bulletin, Alaska Department of Fish and Game.

Hengeveld, P.E. & Festa-Bianchet, M. (2011). Harvest regulations and artificial selection on horn size in male bighorn sheep. The Journal of Wildlife Management, 75, 189-197.

Hester, A.J., Bergman, M., Iason & G.R., Moen, J. (2006). Impacts of large herbivores on plant community structure and dynamics. In: Danell, K., Duncan, P., Bergström, R. & Pastor, J. (Eds.), Large Herbivore Ecology, Ecosystem Dynamics and Conservation. Cambridge University Press, Cambridge, pp. 97-141

Hik, D.S. & Carey, J. (2000). Cohort variation in horn growth of Dall sheep rams in the southwest Yukon, 1969-1999. Biennial Symposium Northern Wild Sheep and Goat Council, 12, 88-100.

Huete, A.R., Jackson, R.D. & Post, D.F. (1985). Spectral response of a plant canopy with different soil backgrounds. Remote Sensing of Environment, 17, 37-53.

Huete, A.R. & Tucker, C.J. (1991). Investigation of soil influences in AVHRR red and near-infrared vegetation index imagery. International Journal of Remote Sensing, 12, 1223-1242.

Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X. & Ferreira, L.G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment, 83, 195-213.

Hurley, M.A., Hebblewhite, M., Gaillard, J.-M., Dray, S., Taylor, K.A., Smith, W.K., … Bonenfant, C. (2014). Functional analysis of normalized difference vegetation index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. Philosophical Transactions of the Royal Society B: Biological Sciences, 369: 20130196.

Jarman, P.J. (1974). The social organisation of antelope in relation to their ecology. Behaviour, 48, 215-266.

Jobling, M. (2010). Are compensatory growth and catch-up growth two sides of the same coin? Aquaculture International, 18, 501-510.

Johnson, K.A. (1997). Trophy hunting as a conservation tool for Caprinae in Pakistan. In: Freese, C.H. (Ed.), Harvesting Wild Species: Implications for Biodiversity Conservation. The John Hopkins University Press, London, pp. 393-423.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994). Organisms as ecosystem engineers. Oikos, 69, 373-386.

Jorgenson, J.T., Festa-Bianchet, M. & Wishart, W.D. (1993). Harvesting bighorn ewes: consequences for population size and trophy ram production. The Journal of Wildlife Management, 57, 429-435.

Jorgenson, J.T., Festa-Bianchet, M. & Wishart, W.D. (1998). Effects of population density on horn development in bighorn rams. The Journal of Wildlife Management, 62, 1011-1020.

Justice, C.O., Townshend, J.R.G., Holben, B.N. & Tucker, C.J. (1985). Analysis of the phenology of global vegetation using meteorological satellite data. International Journal of Remote Sensing, 6, 1271-1318.

Kachel, S.M., McCarthy, K.P., McCarthy, T.M. & Oshurmamadov, N. (2017). Investigating the potential impact of trophy hunting of wild ungulates on snow leopard Panthera uncia conservation in Tajikistan. Oryx, 51, 597-604.

Kardos, M., Luikart, G. & Allendorf, F.W. (2018). Predicting the evolutionary effects of hunting requires an understanding of genetics. The Journal of Wildlife Management, 82, 889-891.

Kelley, C., Ting, M., Seager, R. & Kushnir, Y. (2012). Mediterranean precipitation climatology, seasonal cycle, and trend as simulated by CMIP5. Geophysical Research Letters, 39, L21703.

Köppen, W. (1923). Die Klimate der Erde. Walter de Gruyter & Co., Berlin und Leipzig.

Kottek, M., Grieser, J., Beck, C., Rudolf, B. & Rubel, F (2006). World Map of the Köppen Geiger climate classification updated. Meteorologische Zeitschrift, 15, 259-263.

Kruuk, L.E.B., Slate, J., Pemberton, J.M., Brotherstone, S., Guinness, F. & Clutton-Brock, T. (2002). Antler size in red deer: heritability and selection but no evolution. Evolution, 56, 1683-1695.

Lamy, E., Rawel, H., Schweigert, F.J., Capela e Silva, F., Ferreira, A., Costa, A.R., ... Sales-Baptista, E. (2011). The effect of tannins on Mediterranean ruminant ingestive behavior: the role of the oral cavity. Molecules, 16, 2766-2784.

Landete-Castillejos, T., Garcia, A., Carrion, D., Estevez, J.A., Ceacero, F., Gaspar-Lopez, E. & Gallego, L. (2009). Age-related body weight constraints on prenatal and milk provisioning in iberian red deer (*Cervus elaphus hispanicus*) affect allocation of maternal resources. Theriogenology, 71, 400-407.

Larson, G. & Fuller, D.Q. (2014). The evolution of animal domestication. Annual Review of Ecology, Evolution, and Systematics, 45, 115-136.

Leader-Williams, N. (2009). Conservation and Hunting: friends or foes? In: Dickson, B., Hutton, J. & Adams, W.M. (Eds.), Recreational Hunting, Conservation and Rural Livelihoods. Wiley-Blackwell, Oxford, pp. 9-24.

Leader-Williams, N., Smith, R.J. & Walpole, M.J. (2001). Elephant hunting and conservation, Science, 293, 2203-2204.

Lenormand, T. (2002). Gene flow and the limits to natural selection. Trends in Ecology and Evolution, 17, 183-189.

León-Vizcaíno, L., Ruíz de Ybáñez, M., Cubero, M.J., Ortíz, J.M., Espinosa, J. & Pérez, L. (1999). Sarcoptic mange in Spanish ibex from Spain. Journal of Wildlife Diseases, 35, 647-659.

Leslie, D.M., Bowyer, R.T. & Jenks, J.A. (2008). Facts from feces: nitrogen still measures up as nutritional index for mammalian herbivores. The Journal of Wildlife Management, 72, 1420-1433.

Lindsey, P.A. (2008). Trophy hunting in sub-Saharan Africa: economic scale and conservation significance. Best Practices in Sustainable Hunting, 41-47.

Lindsey, P.A., Alexander, R., Frank, L.G., Mathieson, A. & Romañach, S.S. (2006). Potential of trophy hunting to create incentives for wildlife conservation in Africa where alternative wildlife-based land uses may not be viable. Animal Conservation, 9, 283-291.

Lindsey, P.A., Roulet, P.A. & Romañach, S.S. (2007). Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. Biological Conservation, 134, 455-469.

Lindström, J., Metcalfe, N.B. & Royle, N.J. (2005). How are animals with ornaments predicted to compensate for a bad start in life? A dynamic optimization model approach. Functional Ecology, 19, 421-428.

Little, S.E., Davidson, W.R., Rakich, P.M., Nixon, T.L., Bounous, D.I. & Nettles, V.F. (1998). Responses of red foxes to first and second infestation with *Sarcoptes scabiei*. Journal of Wildlife Diseases, 34, 600-611.

Loe, L.E., C. Bonenfant, A. Mysterud, J.M. Gaillard, R. Langvatn, F. Klein, C., … Stenseth, N.C. (2005). Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. Journal of Animal Ecology, 74, 579-588.

Loehr, J., Carey, J., O'Hara, R.B. & Hik, D.S. (2010). The role of phenotypic plasticity in responses of hunted thinhorn sheep ram horn growth to changing climate conditions. Journal of Evolutionary Biology, 23, 783-790.

López-Olvera, J.R., Serrano, E., Armenteros, A., Pérez, J.M., Fandos, P., Carvalho, J., ... Granados, J.E. (2015). Sex-biased severity of sarcoptic mange at the same biological cost in a sexually dimorphic ungulate. Parasites & Vectors, 8, 583.

Loveridge, A.J., Reynolds, J.C. & Milner-Gulland, E.J. (2006). Does sport hunting benefit conservation? In: Macdonald, D.W., Service, K. (Eds.), Key Topics in Conservation Biology. Blackwell Publishing, Oxford, pp. 224-240.

Mahoney, S.P., Weir, J.N., Luther, G., Schaefer, J.A. & Morrison, S.F. (2011). Morphological change in Newfoundland caribou: effects of abundance and climate. Rangifer, 31, 21-34.

Mairota, P., Leronni, V., Xi, W., Mladenoff, D.J. & Nagendra, H. (2013). Using spatial simulations of habitat modifications for adaptative management of protected areas: Mediterranean grassland modification by woody plant encroachment. Environmental Conservation, 41, 144-156.

Martínez, T. (1989). Recursos tróficos de la cabra montes (*Capra pyrenaica* Schinz, 1938) en la sierra de Gredos durante otoño e invierno. Ecología, 3, 179-186.

Martínez, T. (1994). Dieta estacional de la cabra montés (*Capra pyrenaica*) en los Puertos de Tortosa y Beceite (area Mediterranica del nordeste de España). Ecología, 8, 373-380.

Martínez, T. (2000). Diet selection by Spanish ibex in early summer in Sierra Nevada. Acta Theriologica, 45, 335-346.

Martinez, T., Martinez, E. & Fandos, P. (1985). Composition of the food of the Spanish wild goat in Sierras de Cazorla and Segura, Spain. Acta Theriologica, 30, 461-494.

McLeod, A.I. (2011). Kendall: Kendall rank correlation and Mann-Kendall trend test. R Package Version 2.2. https://cran.r-project.org/web/packages/Kendall/index.html

Merilä, J. & Andrew, A.P. (2014). Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. Evolutionary Applications, 7, 1-14.

Metcalfe, N.B. & Monaghan, P. (2001). Compensation for a bad start: grow now, pay later? Trends in Ecology and Evolution, 16, 254-260.

Mevik, B.H. & Wehrens, R (2007). The pls package: principal components and partial least squares regression in R. Journal of Statistical Software, 18, 1-24.

Milner, J.M., Nilsen, E.B. & Andreassen, H.P. (2006). Demographic side effects of selective hunting in ungulates and carnivores. Conservation Biology, 21, 36-47.

Milner, J.M., Van Beest, F.M., Schmidt, K.T., Brook, R.K. & Storaas, T. (2014). To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates. The Journal of Wildlife Management, 78, 1322-1334.

Min, B.R. & Hart, S.P. (2003). Tannins for suppression of internal parasites. Journal of Animal Science, 81, 102-109.

Miranda, M., Sicilia, M., Bartolomé, J., Molina-Alcaide, E., Gálvez-Bravo, L., Cassinello, J. (2012). Foraging sexual segregation in a Mediterranean environment: summer drought modulates sex-specific resource selection. Journal of Arid Environments, 85, 97-104.

Moço, G., Guerreiro, M., Ferreira, A.F., Rebelo, A., Loureiro, A., Petrucci-Fonseca, F. & Pérez, J.M. (2006). The ibex *Capra pyrenaica* returns to its former Portuguese range. Oryx, 40, 351-354.

Monteith, K.L., Bleich, V.C., Stephenson, T.R., Pierce, B.M., Conner, M.M., Kie, J.G. & Bowyer, R.T. (2014). Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs, 186, 1-62.

Monteith, K.L., Long, R.A., Bleich, V.C., Heffelfinger, J.R., Krausman, P.R. & Bowyer, R.T. (2013). Effects of harvest, culture, and climate on trends in size of horn-like structures in trophy ungulates. Wildlife Monographs, 183, 1-26.

Monteith, K.L., Long, R.A., Stephenson, T.R., Bleich, V.C., Bowyer, R.T. & Lasharr, T.N. (2018). Horn size and nutrition in mountain sheep: Can ewe handle the truth? The Journal of Wildlife Management, 82, 67-84.

Mounsey, K.E., Murray, H.G., Bielefeld-Ohmann, H., Pasay, C., Holt, D.C., Currie, B.J., … McCarthy, J.S. (2015). Prospective study in a porcine model of *Sarcoptes scabiei* indicates the association of Th2 and Th17 pathways with the clinical severity of scabies. PLOS Neglected Tropical Diseases, 9, e0003498.

Mutanga, O. & Skidmore, A.K. (2004). Integrating imaging spectroscopy and neural networks to map grass quality in the Kruger National Park, South Africa. Remote Sensing of Environment, 90, 104-115.

Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. & Nemani, R.R. (1997). Increased plant growth in the northern high latitudes from 1981 to 1991. Nature, 386, 698-702.

Mysterud, A. & Bischof, R. (2010). Can compensatory culling offset undesirable evolutionary consequences of trophy hunting? Journal of Animal Ecology, 79, 148-160.

Mysterud, A. (2014). Effects of selective harvesting on ungulate populations. In: Putman, R. & Apollonio, M. (Eds.), Behaviour and Management of European Ungulates. Whittles Publishing, Caithness, pp. 124-147.

Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution, 4, 133-142.

Nelson, P.R., Roland, C., Macander, M.J. & McCune, B. (2013). Detecting continuous lichen abundance for mapping winter caribou forage at landscape spatial scales. Remote Sensing of Environment, 137, 43-54.

Nimmervoll, H., Hoby, S., Robert, N., Lommano, E., Welle, M. & Ryser-Degiorgis, M.P. (2013). Pathology of sarcoptic mange in red foxes (*Vulpes vulpes*): macroscopic and histologic characterization of three disease stages. Journal of Wildlife Diseases, 49, 91-102.

Ogutu, Z.A. (2002). The impact of ecotourism on livelihood and natural resource management in Eselenkei, Amboseli ecosystem, Kenya. Land Degradation and Development, 13, 251-256.

Oleaga, A., Casais, R., González-Quirós, P., Prieto, M. & Gortázar, C. (2008). Sarcoptic mange in red deer from Spain: Improved surveillance or disease emergence? Veterinary Parasitology, 154, 103-113.

Ordiz, A., Bischof, R. & Swenson, J.E. (2013). Saving large carnivores, but losing the apex predator? Biological Conservation, 168, 128-133.

Owen-Smith, N. & Mills, M.G.L. (2006). Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. Ecological Monographs, 76, 73-92.

Palazy, L., Bonenfant, C., Gaillard, J.-M. & Courchamp, F. (2011). Rarity, trophy hunting and ungulates. Animal Conservation, 15, 4-11.

Palkovacs, E.P., Moritsch, M.M., Contolini, G.M. & Pelletier, F. (2018). Ecology of harvest-driven trait changes and implications for ecosystem management. Frontiers in Ecology and the Environment, 16, 20-28.

Parker, K.L., Barboza, P.S. & Gillingham, M.P. (2009). Nutrition integrates environmental responses of ungulates. Functional Ecology, 23, 57-69.

Paruelo, J.M., Epstein, H.E., Lauenroth, W.K. & Burke, I.C. (1997). ANPP estimates from NDVI for the Central Grassland Region of the United States. Ecology, 78, 953-958.

Pelletier, F., Festa-Bianchet, M. & Jorgenson, J.T. (2012). Data from selective harvests underestimate temporal trends in quantitative traits. Biology Letters, 8, 878-881.

Pelletier, F., Festa-Bianchet, M., Jorgenson, J.T., Feder, C. & Hubbs, A. (2014). Can phenotypic rescue from harvest refuges buffer wild sheep from selective hunting? Ecology and Evolution, 4, 3375-3382.

Pence, D.B., Windberg, L.A., Pence, B.C. & Sprowls, R. (1983). The epizootiology and pathology of sarcoptic mange in coyotes Canis latrans from south Texas. Journal of Parasitology, 69, 1100-1115.

Pence, D.B. & Ueckerman, E. (2002). Sarcoptic mange in wildlife. Revue scientifique et technique (International Office of Epizootics), 21, 385-398.

Peñuelas J., Sardans, J., Filella, I., Estiarte, M., Llusià, J, Ogaya., … Terradas, J. (2017). Impacts of global change on Mediterranean forests and their services. Forests, 8, 463.

Perea, R., Girardello, M. & San Miguel, A. (2014). Big game or big loss? High deer densities are threatening woody plant diversity and vegetation dynamics. Biodiversity and Conservation, 23, 1303-1318.

Perea, R., Perea-García-Calvo, R., Díaz-Ambrona, C.G. & San Miguel, A. (2015). The reintroduction of a flagship ungulate *Capra pyrenaica*: Assessing sustainability by surveying woody vegetation. Biological Conservation, 181, 9-17.

Pérez, J.M., Granados, J.E., Soriguer, R.C., Fandos, P., Márquez, F.J. & Crampe, J.P. (2002). Distribution, status and conservation problems of the Spanish Ibex, *Capra pyrenaica* (Mammalia: Artiodactyla). Mammal Review, 32, 26-39.

Pérez, J.M., Meneguz, P.G., Dematteis, A., Rossi, L. & Serrano, E. (2006). Parasites and conservation biology: the “ibex-ecosystem”. Biodiversity and Conservation, 15, 2033-2047.

Pérez, J.M., Granados, J.E., Sarasa, M., Serrano, E. (2011a). Usefulness of estimated surface area of damaged skin as a proxy of mite load in the monitoring of sarcoptic mange in free-ranging populations of Iberian wild goat, *Capra pyrenaica*. Veterinary Parasitology, 176, 258-264.

Pérez, J.M., Serrano, E., González-Candela, M., León-Vizcaino, L., Barberá, G.G., de Simón, M.A., ... Festa-Bianchet, M. (2011b). Reduced horn size in two wild trophy-hunted species of *Caprinae*. Wildlife Biology, 17, 102-112.

Pérez, J.M., Serrano, E., Soriguer, R.C., González, F.J., Sarasa, M., Granados, J.E., ... Fandos, P. (2015). Distinguishing disease effects from environmental effects in a mountain ungulate: seasonal variation in body weight, hematology, and serum chemistry among Iberian ibex (*Capra pyrenaica*) affected by sarcoptic mange. Journal of Wildlife Diseases., 51, 148-156.

Pérez-Barbería, F.J., Robles, L. & Nores, C. (1996). Horn growth pattern in Cantabrian chamois *Rupicapra pyrenaica parva*: influence of sex, location and phaenology. Acta theriologica, 41, 83-92.

Pérez-Luque, A.J., Bonet, F.J., Pérez-Pérez, R., Aspizua, R., Lorite, J. & Zamora, R. (2014). Sinfonevada: Dataset of Floristic diversity in Sierra Nevada forests (SE Spain). PhytoKeys, 35, 1-15.

Pettorelli, N., Mysterud, A., Yoccoz, N.G., Langvatn, R. & Stenseth, N.C. (2005). Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. Proceedings of the Royal Society of London B: Biological Sciences, 272, 2357-2364.

Pettorelli, N. (2013). The Normalized Difference Vegetation Index. Oxford University Press, Oxford.

Pettorelli, N., Laurance, W.F., O'Brien, T.G., Wegmann, M., Nagendra, H. & Turner, W. (2014). Satellite remote sensing for applied ecologists: opportunities and challenges. Journal of Applied Ecology, 51, 839-848.

Pidancier, N., Jordan, S., Luikart, G. & Taberlet, P. (2006). Evolutionary history of the genus *Capra* (Mammalia, Artiodactyla): Discordance between mitochondrial DNA and Y-chromosome phylogenies. Molecular Phylogenetics and Evolution, 40, 739-749.

Pigeon, G., Festa-Bianchet, M., Coltman, D.W. & Pelletier, F. (2016). Intense selective hunting leads to artificial evolution in horn size. Evolutionary Applications, 9, 521-530.

Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. (2012). nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3. http://CRAN.R-project.org/package=nlme.

Plard, F., Gaillard, J.-M., Coulson, T., Hewison, A.J.M., Delorme, D., Warnant, C. & Bonenfant, C. (2014). Mismatch between birth date and vegetation phenology slows the demography of roe deer. Plos Biology, 12, e1001828.

Putman, R., Apollonio, M. & Andersen, R. (2011). Ungulate Management in Europe: Problems and Practices. Cambridge University Press, New York.

Quan, C., Han, S., Utescher, T., Zhang, C. & Liu, Y.-S. (2013). Validation of temperature–precipitation based aridity index: Paleoclimatic implications. Palaeogeography, Palaeoclimatology, Palaeoecology, 386, 86-95.

Quirós-Fernández, F., Marcos, J., Acevedo, P. & Gortázar, C. (2017). Hunters serving the ecosystem: the contribution of recreational hunting to wild boar population control. European Journal of Wildlife Research, 63:57.

R Development Core Team (2017). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. http://www.R-project.org/.

Råberg, L., Graham, A.L. & Read, A.F. (2009). Decomposing health: tolerance and resistance to parasites in animals. Philosophical Transactions of the Royal Society B: Biological Sciences, 364, 37-49.

Ramanzin, M., Aguado, M.A.P., Ferragina, A., Sturaro, E., Semenzato, P., Serrano, E., ... Bittante, G. (2017). Methodological considerations for the use of faecal nitrogen to assess diet quality in ungulates: The Alpine ibex as a case study. Ecological Indicators, 82, 399-408.

Rands, S.A., Evans, M.R. & Johnstone, R.A. (2011). The dynamics of honesty: modelling the growth of costly, sexually-selected ornaments. Plos One, 6, e27174.

Reed, J.L. & McCarthy, B.C. (1996). Patterns of leaf tannin variation in chestnut oak (*Quercus prinus*) and black oak (*Quercus velutina*) with respect to topography in a southeastern Ohio oak-hickory forest. Bulletin of the Torrey Botanical Club, 123, 243-248.

Refoyo, P., Olmedo, C. & Muñoz, B. (2016). Space use of a reintroduced population of Iberian ibex (*Capra pyrenaica*) in a protected natural area. Canadian Journal of Zoology, 94, 181-189.

Reynolds, P. & Staines, B. (1997) Deer management in Scotland. In: Bolton, M. (Ed.), Conservation and the Use of Wildlife Resources. Chapman & Hall, London, pp. 171-190.

Ripley, B. (2017). boot: Bootstrap Functions. R Package Version 1.3-20. https://cran.r-project.org/web/packages/boot/.

Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., ... Valkenburgh, B.V. (2015). Collapse of the world's largest herbivores. Science Advances, 1, e1400103.

Røed, K.H., Holand, Ø., Mysterud, A., Tverdal, A, Kumpula, J. & Nieminen, M. (2007). Male phenotypic quality influences offspring sex ratio in a polygynous ungulate. Proceedings of the Royal Society of London B: Biological Sciences, 274, 727-733

Rossi, L., Meneguz, P.G., De Martin P. & Rodolfi, M. (1995). The epizootiology of sarcoptic mange in chamois, *Rupicapra rupicapra*, from the Italian eastern Alps. Parasitologia, 37, 233-240.

Rossi, S., Fromont, E., Pontier, D., Crucière, C., Hars, J., Barrat, J., Pacholek, X. & Artois, M. (2005). Incidence and persistence of classical swine fever in free-ranging wild boar (*Sus scrofa*). Epidemiology & Infection, 133, 559-568.

Ruckstuhl, K.E. & Neuhaus, P. (2000). Sexual segregation in ungulates: a new approach. Behaviour, 137, 361-377.

Rundel, P.W., Arroyo, M.T.K., Cowling, R.M., Keeley, J.E., Lamont, B.B. & Vargas, P. (2016). Mediterranean biomes: evolution of their vegetation, floras, and climate. Annual Review of Ecology, Evolution, and Systematics, 47, 383-407.

Rutter, C. (1902). Natural history of the Quinnat salmon: a report of investigations in the Sacramento River, 1886–1901. Bulletin of the US Fish Commission, 22, 65-141.

Ryan, S.J., Cross, P.C., Winnie, J., Hay, C., Bowers, J. & Getz, W.M. (2012). The utility of normalized difference vegetation index for predicting African buffalo forage quality. The Journal of Wildlife Management, 76, 1499-1508.

Sanchez, G. (2013). PLS Path Modeling with R. Trowchez Editions. Berkeley.

Sanchez, G., Trinchera, L. & Russolillo, G. (2015). plspm: Tools for Partial Least Squares Path Modeling (PLS-PM). R Package Version 0.4.9 http://cran.r-project.org/web/packages/plspm/index.html.

Santiago-Moreno, J., Gómez-Brunet, A., Toledano-Díaz, A., Salas-Veja, R., Gómez-Guillamón, F. & López-Sebastián, A. (2012). Role of testosterone and photoperiod on seasonal changes in horn growth and sperm variables in the Iberian ibex: a model for polygynous wild bovids. Journal of Endocrinology, 214, 155-163.

Santos, J.P.V., Vincente, J., Carvalho, J., Queirós, J., Villamuelas, M., Albanell, E., ... Fonseca, C. (2018). Determining changes in the nutritional condition of red deer in Mediterranean ecosystems: Effects of environmental, management and demographic factors. Ecological Indicators, 87, 261-271.

Sarasa, M. (2013). Trophy hunting, size, rarity and willingness to pay: inter–specific analyses of trophy prices require reliable specific data. Animal Biodiversity and Conservation, 36, 165-175.

Sarasa, M., Rambozzi, L., Rossi, L., Meneguz, P.G., Serrano, E., Granados, J.E., González, F.J., Fandos, P., Soriguer, R.C., González, G., Joachim, J. & Pérez, J.M. (2010). *Sarcoptes scabiei*: specific immune response to sarcoptic mange in the Iberian ibex *Capra pyrenaica* depends on previous exposure and sex. Experimental Parasitology, 124, 265-271.

Sarasa, M., Serrano, E., Soriguer, R.C., Granados, J.E., Fandos, P., Gonzalez, G., Joachim, J. & Pérez, J.M. (2011). Negative effect of the arthropod parasite, *Sarcoptes scabiei*, on testes mass in Iberian ibex, *Capra pyrenaica*. Veterinary Parasitology, 175, 306-312.

Sarasa, M., Soriguer, R.C., Granados, J.E., Casajus, N. & Pérez, J.M. (2012). Mismeasure of secondary sexual traits: an example with horn growth in the Iberian ibex. Journal of Zoology, 288, 170-176.

Schweiger, A.K., Risch, A.C., Damm, A., Kneubühler, M., Haller, R., Schaepman, M.E., Schütz, M. (2014). Using imaging spectroscopy to predict above-ground plant biomass in alpine grasslands grazed by large ungulates. Journal of Vegetation Science. 26, 175-90.

Schweiger, A.K., Schütz, M., Anderwald, P., Schaepman, M.E., Kneubühler, M., Haller, R. & Risch, A.C. (2015). Foraging ecology of three sympatric ungulate species – Behavioural and resource maps indicate differences between chamois, ibex and red deer. Movement Ecology, 3:6.

Scooter, G.W. (1980). Management of wild ungulate habitat in the western United States and Canada: A review. Journal of Range Management, 33, 16-27.

Seager, R., Liu, H., Henderson, N., Simpson, I., Kelley, C., Shaw, T., Kushnir, Y. & Ting, M. (2014). Causes of increasing aridification of the Mediterranean region in response to rising greenhouse gases. Journal of Climate, 27, 4655-4676.

Serrano, E., Pérez, J.M., Christiansen, P. & Gállego, L. (2006). Sex-difference in the ossification rate of the appendicular skeleton in *Capra pyrenaica* Schinz, 1838, and its utility in the sex identification of long bones. Anatomia, Histologia, Embryologia, 35, 69-75.

Serrano, E., Granados, J.E. & Pérez, J.M. (2007). Sarcoptic mange and metapodial development in growing male Iberian ibex (*Capra pyrenaica*). Veterinary Parasitology, 144, 375-379.

Serrano, E., Alpizar-Jara, R., Morellet, N. & Hewison, A.J.M. (2008). A half a century of measuring ungulate body condition using indices: is it time for a change? European Journal of Wildlife Research, 54, 675-680.

Serrano, E., González, F.J., Granados, J.E., Moço, G., Fandos, P., Soriguer, R.C. & Pérez, J.M. (2008). The use of total serum proteins and tryglycerides for monitoring body condition in the Iberian wild goat (*Capra pyrenaica*). Journal of Zoo and Wildlife Medicine, 39, 646–649.

Serrano, E., Granados, J.E., Sarasa, M., González, F.J., Fandos, P., Soriguer, R.C. & Pérez, J.M. (2011). The effects of winter severity and population density on body stores in the Iberian wild goat (*Capra pyrenaica*) in a highly seasonal mountain environment. European Journal of Wildlife Research, 57, 45-55.

Shackleton, D.M. (1997). Wild sheep and goats and their relatives: status survey and conservation action plan for *Caprinae*. International Union for Conservation of Nature, Gland.

Simard, A., Huot, J., Bellefeuille, S. & Côté, S.D. (2014). Influences of habitat composition, plant phenology, and population density on autumn indices of body condition in a northern white-tailed deer population. Wildlife Monographs, 187, 1-28.

Simon, A. (2017). The competitive consumption and fetishism of wildlife trophies. Journal of Consumer Culture. DOI: 10.1177/1469540517690571.

Skerratt, L.F., Middleton, D. & Beveridge, I. (1999). Distribution of life cycle stages of *Sarcoptic scabiei* var. *wombati* and effects of severe mange on common wombats in Victoria. Journal of Wildlife Diseases, 35, 633-646.

Skidmore, A.K., Ferwerda, J.G., Mutanga, O., Van Wieren, S.E., Peel, M., Grant, R.C., … Venus, V. (2010). Forage quality of savannas — Simultaneously mapping foliar protein and polyphenols for trees and grass using hyperspectral imagery. Remote Sensing of Environment, 114, 64-72.

Solano, R., Didan, K., Jacobson, A. & Huete, A. (2010). MODIS vegetation index user's guide (MOD13 Series). Vegetation Index and Phenology Lab, The University of Arizona.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & van der Linde, A. (2002). Bayesian measures of model complexity and model fit. Journal of the Royal Statistical Society. Series B, 64, 583-639.

Steele, B.M. & Hogg, J.T. (2003). Measuring individual quality in conservation and behavior. In: Festa-Bianchet, M., Apollonio, M. (Eds.), Animal Behavior and Wildlife Conservation. Island Press, Washington, D.C., pp. 243-269.

Stoffel, M., Nakagawa, S. & Schielzeth, H. (2018). rptR: Repeatability estimation for Gaussian and non-Gaussian data. R Package Version 0.9.21 https://cran.r-project.org/web/packages/rptR/index.html.

Tenenhaus, M., Vinzi, V.E., Chatelin, Y.-M. & Lauro, C. (2005). PLS path modeling. Computational Statistics & Data Analysis, 48, 159-205.

Therrien, J.F., Côté, S.D., Festa-Bianchet, M. & Ouellet, J.P. (2008). Maternal care in white-tailed deer: trade-off between maintenance and reproduction under food restriction. Animal Behaviour, 75, 235-243.

Toïgo, C., Gaillard, J.-M. & Michallet, J. (1999). Cohort affects growth of males but not females in Alpine ibex (*Capra ibex*). Journal of Mammalogy, 80, 1021-1027.

Toïgo, C., Gaillard, J.-M. & Loison, A. (2013). Alpine ibex males grow large horns at no survival cost for most of their lifetime. Oecologia, 173, 1261-1269.

Toledano-Díaz, A., Santiago-Moreno, J., Gómez-Brunet, A., Pulido-Pastor,A. & López-Sebastián, A. (2007). Horn growth related to testosterone secretion in two wild Mediterranean ruminant species: The Spanish ibex (*Capra pyrenaica hispanica*) and European mouflon (*Ovis orientalis musimon*). Animal Reproduction Science, 102, 300-307.

Trimble, M.J., Ferreira, S.M. & Van Aarde, R.J. (2009), Drivers of megaherbivore demographic fluctuations: inference from elephants. Journal of Zoology, 279, 18-26.

U.S. Fish and Wildlife Services (2014). Successful conservation efforts result in reclassification of rare Pakistani mountain goat under the endangered species act. https://www.fws.gov/news/ShowNews.cfm?ID=E6D8E1A2-FF83-1C13-22322580A454755D (Accessed on 14 December 2017).

Valente, A., Valente, J., Fonseca, C. & Torres, R. (2017). The success of species reintroductions: a case study of red deer in Portugal two decades after reintroduction. International Journal of Biodiversity Science, Ecosystem Services & Management, 13, 134-138.

Van Soest, P.J. (1994). Nutritional Ecology of the Ruminant, Second ed. Cornell University Press, New York.

Vargas, D. & Vila, J. (2005). Ecología del paisaje y sistemas de información geográfica ante el cambio socioambiental en las áreas de montaña mediterránea. Una aproximación metodológica al caso de los valles d'Hortmoier y Sant Aniol (Alta Garrotxa, Girona). Revista Internacional de Ciencias Sociales, 25.

Viana, D.S., Granados, J.E., Fandos, P., Pérez, J.M., Cano-Manuel, F.J., Burón, D., ... Soriguer, R.C. (2018). Linking seasonal home range size with habitat selection and movement in a mountain ungulate. Movement Ecology, 6, 1.

Villamuelas, M., Fernández, N., Albanell, E., Gálvez-Cerón, A., Bartolomé, J., Mentaberre, G., ... Serrano, E. (2016). The Enhanced Vegetation Index (EVI) as a proxy for diet quality and composition in a mountain ungulate. Ecological Indicators, 61, 658-666.

von Hardenberg, A., Bassano, B., Arranz, M.P.Z. & Bogliani, G. (2004). Horn growth but not asymmetry heralds the onset of senescence in male Alpine ibex (*Capra ibex*). Journal of Zoology, 263, 425-432.

Wang, Z., Yang, R.C., Goonewardene, L.A. & Huedepohl, C. (1999). Genetic analysis of velvet antler yield in farmed elk (*Cervus elaphus*). Canadian Journal of Animal Science, 79, 569-571.

Willisch, C.S. & Neuhaus, P. (2009). Alternative mating tactics and their impact on survival in adult male Alpine ibex (*Capra ibex*). Journal of Mammalogy, 90, 1421-1430.

Willisch, C.S. & Neuhaus, P. (2010). Social dominance and conflict reduction in rutting male Alpine ibex, *Capra ibex*. Behavioral Ecology, 21, 372-380.

Wood, D. (2012). mgcv: Mixed GAM Computation Vehicle with GCV/AIC/REML Smoothness Estimation. R Package Version 1.7.22. https://CRAN.R-project.org/package=mgcv.

Wood, S. & Scheipl, F. (2016). gamm4: Generalized Additive Mixed Models using 'mgcv' and 'lme4'. R Package Version 0.2-4. https://CRAN.R-project.org/package=gamm4.

Zuur, A., Ieno, E. N. & Walker, N. (2009). Mixed effects models and extensions in ecology with R. Springer, New York.

Supplementary material

Supplementary material for the chapter 4 – Habitat management is key to the sustainability of trophy hunting in Mediterranean ecosystems

Appendix A

Fecal samples were collected directly from the rectum of 97 male ibexes between December 2014 and May 2016 (**Figure S1**). We collected 34 fecal samples during the spring (21st March – 20th June), 7 during the summer (21st June – 20th September), 24 during the Autumn (21st September – 20th December) and 32 during the winter (21st December – 20th March). The fecal samples collected during the summer and autumn were pooled in one category due to the low number of samples collected in the summer (Sum-Aut). The place where the fecal samples were collected was georeferenced using a GPS device. The fecal samples were placed in individual plastic zip bags and transported in a cooler box to the laboratory, where they were stored in a freezer at - 20°C. The fecal nitrogen (FN) was used as a proxy of diet quality (Leslie *et al*., 2008) and assessed by using near-infrared reflectance spectroscopy (NIRS). The 94 milled samples were thawed and packed into 35 mm diameter circular cups, with quartz glass window, and scanned from 1100 to 2500 nm using a NIRSystems 5000 scanning monochromator (FOSS, Hillerod, Denmark). Reflectance was recorded at 2 nm intervals as log (1/R), where R represents reflected energy. Each sample was scanned twice, by manually rotating the same cup relative to the previous scan. As the amount of FN excreted can be influenced by other dietary components (Carpio *et al*., 2015), such as fibres and tannins, we also determined the neutral detergent fibre (NDF), the acid detergent fibre (ADF) and the acid detergent lignin (ADL). Here, we expressed the FN as a proportion of NDF (Ramanzin *et al*., 2017).

The relationship between FN values and habitat structure (coniferous forests, shrubs and herbaceous associations and natural pastures) were analyzed by season because the diet composition of the male ibexes is expected to vary over the year (Martínez, 1994) and spring reflects diet quality during horn growth (Fandos & Vigal, 1988). The habitat structure was inferred for a buffer area centered at the sample location. The buffer area (~550

hectares) was defined based on the minimum home range for the species (Escos & Alados, 1992; Viana *et al*., 2018).

The amount of FN varied between 1.6 and 3.7% (average ± SE: 2.3 ± 0.5%) throughout the study period being higher during the spring (average ± SE: 2.7 ± 0.5%) and lower during the summer-autumn (average ± SE: 2.1 ± 0.2%) (**Table S1**).

Table S.1. Parameter estimates for the linear models relating the fecal nitrogen as a proportion of neutral detergent fibre ((FN/NDF)*100) to habitat structure in male ibexes from the *Els Ports de Tortosa i Beseit* National Hunting Reserve, northeastern Spain. Statistically significant results are highlighted in bold.

Season	Habitat structure (%)	Estimate	Std. error	t value	p-value
Spring	Coniferous forests	-0.010	0.010	-1.129	0.267
	Shrubs	0.035	0.026	1.372	0.180
	Natural pastures	0.081	0.035	2.301	<0.05
Sum-Aut	Coniferous forests	0.0001	0.008	0.10	0.921
	Shrubs	-0.0001	0.012	-0.056	0.956
	Natural pastures	-0.002	0.019	-0.085	0.933
Winter	Coniferous forests	-0.002	0.010	-0.143	0.888
	Shrubs	0.030	0.023	1.274	0.213
	Natural pastures	0.017	0.029	0.574	0.571

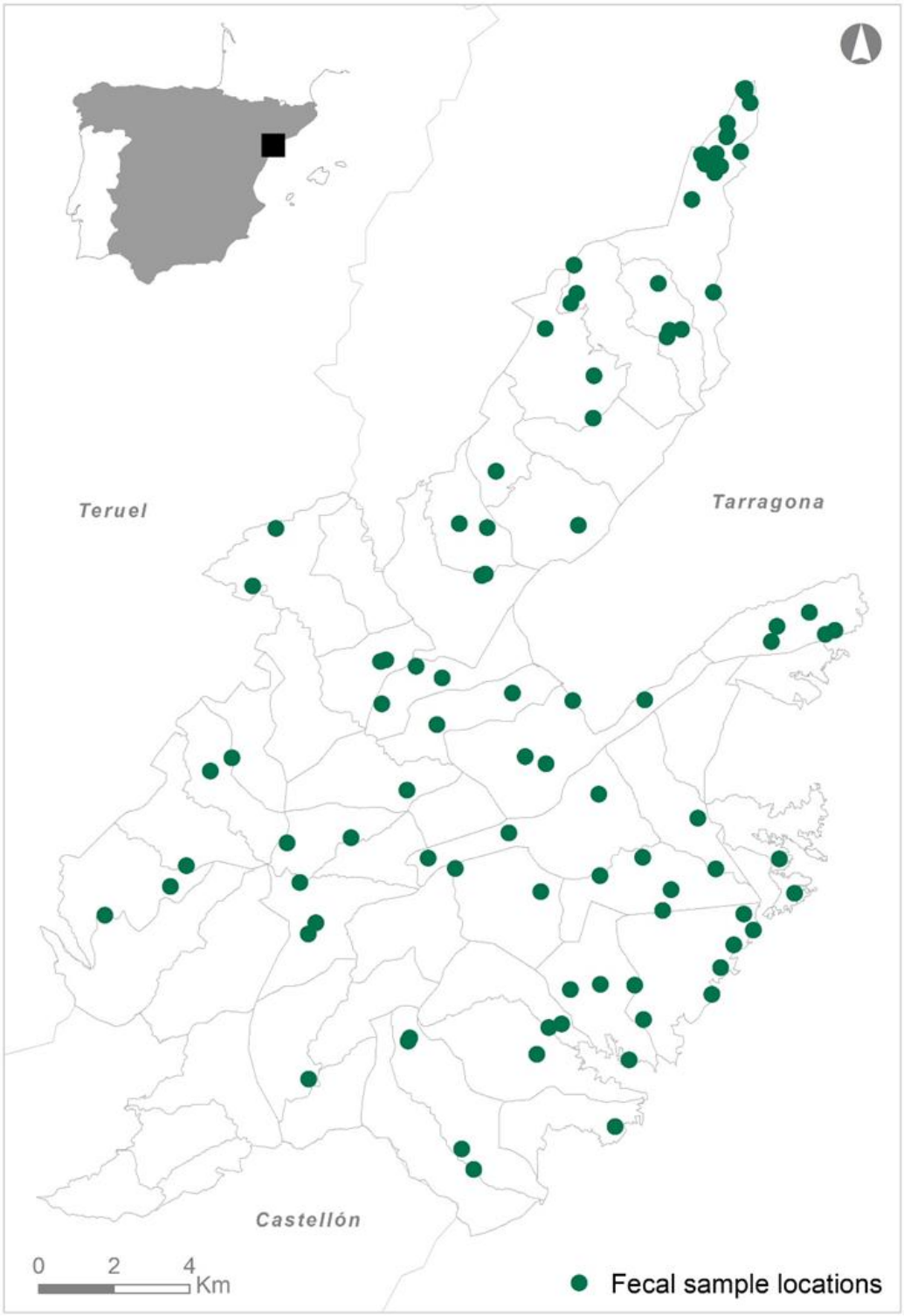

Figure S.1. Location of 97 fecal samples collected in *Els Ports de Tortosa i Beseit* National Hunting Reserve, northeastern Spain, between December 2014 and May 2016.

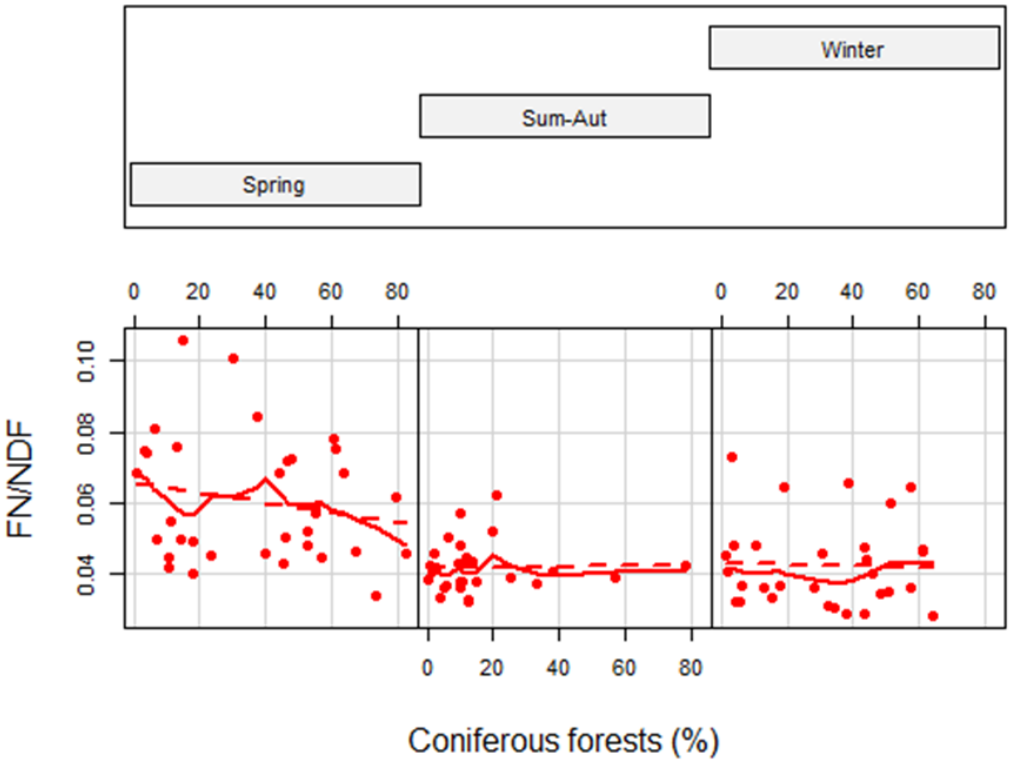

Figure S.2. Seasonal relationship between fecal nitrogen as a proportion of neutral detergent fibre (FN/NDF) and the percentage of coniferous forests.

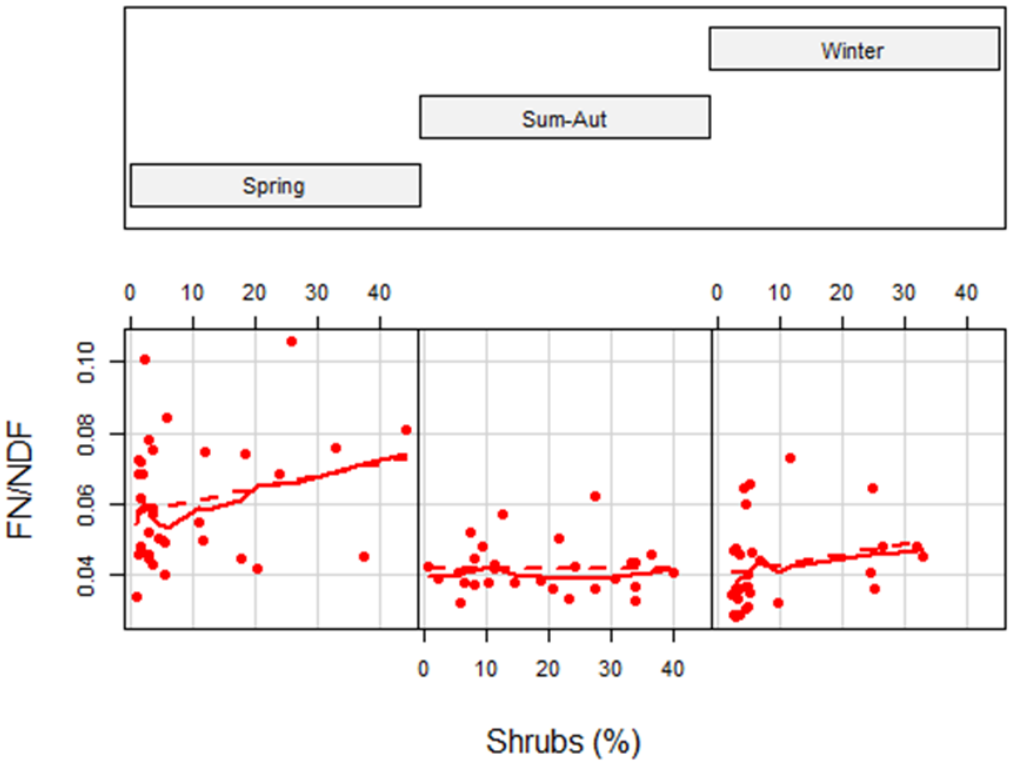

Figure S.3. Seasonal relationship between fecal nitrogen as a proportion of neutral detergent fibre (FN/NDF) and the percentage of shrubs.

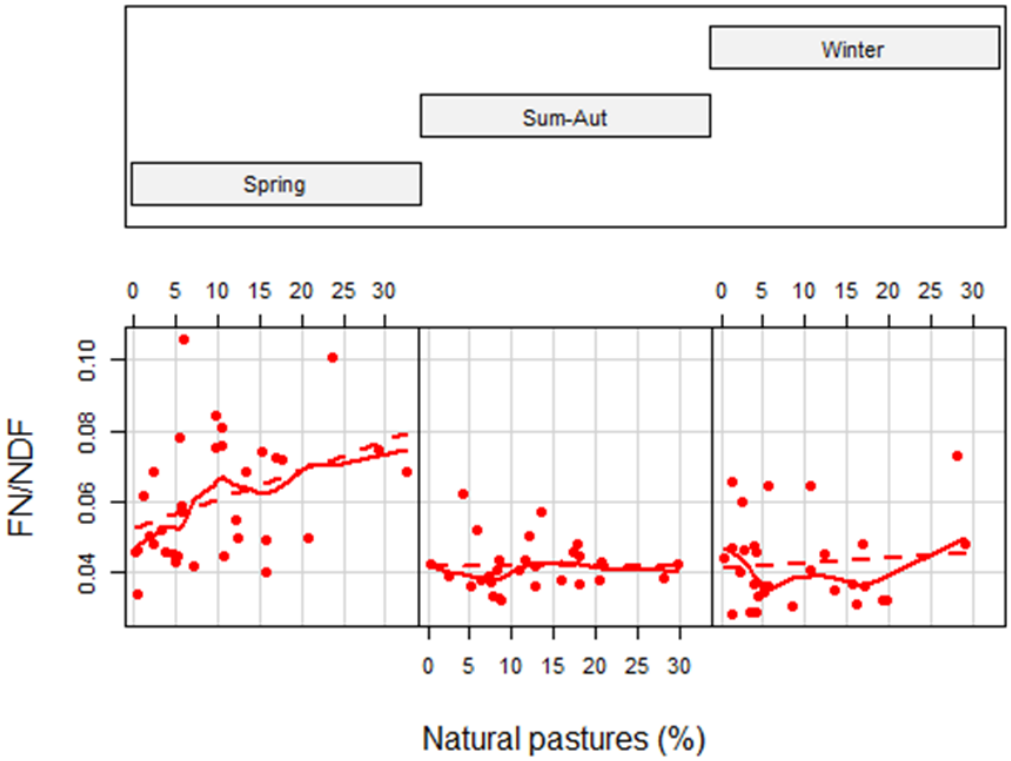

Figure S.4. Seasonal relationship between fecal nitrogen as a proportion of neutral detergent fibre (FN/NDF) and the percentage of natural pastures.

References

Carpio, A.J., Guerrero-Casado, J., Ruiz-Aizpurua, L., Tortosa, F.S. & Vicente, J. (2015). Interpreting faecal nitrogen as a non-invasive indicator of diet quality and body condition in contexts of high ungulate density. European Journal of Wildlife Research, 61, 557-562.

Escos, J. & Alados, C.L. (1992). The home-range of the Spanish ibex in spring and fall. Mammalia, 56, 57-63.

Fandos, P. & Vigal, C.R. (1988). Body weight and horn length in relation to age of the Spanish wild goat. Acta Theriologica, 33, 339-344.

Leslie, D.M., Bowyer, R.T. & Jenks, J.A. (2008). Facts from feces: nitrogen still measures up as nutritional index for mammalian herbivores. Journal of Wildlife Management, 72, 1420-1433.

Ramanzin, M., Aguado, M.A.P., Ferragina, A., Sturaro, E., Semenzato, P., ... Bittante, G. (2017). Methodological considerations for the use of faecal nitrogen to assess diet quality in ungulates: The Alpine ibex as a case study. Ecological Indicators, 82, 399-408.

Viana, D.S., Granados, J.E., Fandos, P., Pérez, J.M., Cano-Manuel, F.J., Burón, D., ... Soriguer, R.C. (2018). Linking seasonal home range size with habitat selection and movement in a mountain ungulate. Movement Ecology, 6:1.

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